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PREDATORY ECOLOGY OF NATICID GASTROPODS WITH A REVIEW OF SHELL BORING PREDATION

Alan R. Kabat

Museum of Comparative Zoology, Harvard University,
Cambridge, Massachusetts 02138 U.S.A.

ABSTRACT

This review provides a critical synthesis and analysis of the extensive body of knowledge of predation by the Naticidae, a cosmopolitan family of burrowing marine gastropods. First, the diversity of shell boring predation is reviewed and documented for ten taxa (nine marine, one terrestrial), in order to facilitate comparative analyses. These predators are: Naticidae, Muricidae, Cassidae and Capulidae (Gastropoda, Prosobranchia); *Okadaia* (Gastropoda, Opisthobranchia); *Aegopinella* (Gastropoda, Pulmonata); *Octopus* (Cephalopoda); *Pseudostylochus* (Turbellaria); Nematoda; and *Asemichthys* (Pisces). Second, the proximate mechanisms of naticid predation are explicated. Third, the known prey of naticids are tabulated; over 80 families of gastropods and bivalves are subject to naticid predation which is essentially restricted to soft-substrate prey taxa. Fourth, the fossil record of naticid predation is summarized; this predation dates from the Cretaceous, with a possible boring "experiment" in the early Triassic. The diagnostic countersunk naticid boreholes are recognizable in fossil and Recent faunas; naticid predation is a readily documented aspect of the otherwise elusive soft-bottom food web. Fifth, the studies on physiology and ecology of naticid predation are integrated into a conceptual framework. These aspects of naticid predation (energy budgets, prey size and species choice, unsuccessful predation) indicate a successful albeit rather stereotyped mode of predation. The macroevolutionary implications (escalation, or "arms races") suggest generalized predator-prey coevolution.

Key words: Naticidae, predation, boring.

DIVERSITY OF BORING PREDATION

In the Mollusca, many of the post-Paleozoic Gastropoda are predators, and an extensive body of research has developed around various aspects of predation by mollusks (Kohn, 1983). Most of these studies treat Recent mollusks, including the community ecology, behavior and physiology of predation. Other, more restricted, studies on fossils analyzed those elements of predation revealed by fossil shells (boreholes and other signs of shell damage and repair) (Kohn, 1985). Among the predatory gastropods, several families include shell borers which excavate a hole in the prey shell to provide access to the prey flesh. Earlier overviews of boring by gastropods by Fischer (1922, 1966), Carriker (1961), Fatton & Roger (1968), Sohl (1969), Bishop (1975), Boucot (1981: 200 ff.), Bromley (1981), Benton (1986) and Vermeij (1987) have summarized some of this research. More general reviews of gastropod feeding biology were provided by Ankel (1938), Fretter & Graham (1962: 240–262), Taylor et al. (1980), Kohn (1983) and Tsikhon-Lukanina (1987). Inevitably, numerous previous studies have been overlooked by subsequent researchers; this paper seeks to provide some unity and a coherent framework to the body of knowledge of shell boring predation by gastropods of the family Naticidae.

The objectives of this paper are: (1) to document the diversity of shell boring predation and related phenomena; (2) to summarize the mechanical or proximate aspects of naticid prey capture and boring; (3) to tabulate the known naticid prey taxa in order to indicate the prey diversity in relation to the overall diversity of marine mollusks; (4) to review the fossil record of naticid predation in the Mesozoic and Cenozoic; and (5) to integrate and synthesize the ecological and evolutionary aspects of naticid predation into a broader conceptual framework.

The diversity of molluscan shell boring predators is briefly reviewed, in order to be able to distinguish amongst the traces of predation left by the various taxonomic groups of predators. Based on this review, it is obvious that predation by boring in taxa other than the Naticidae and Muricidae is seldom studied.

Shell breaking predators, particularly crustaceans and fish, represent an entire field of study in themselves; valuable reviews are provided by Vermeij (1978, 1983c). Not mentioned herein are the diverse groups of symbiotic (non-predatory) epibionts and endolithic shell burrowers, such as certain cyanobacteria, fungi, algae, sponges, polychaetes, sipunculans, barnacles, lithophagid and pholadid bivalves, brachiopods and bryozoans (reviewed by Boekschoten, 1966, and the 1969 *American Zoologist* [vol. 9, #3] symposium on calcibiocavitology). Generally speaking, the latter "bore holes" can be recognized by their large number on a single shell, the lack of complete penetration, and their obvious burrowing aspect. An exception is the pedicle attachment scar of brachiopods, which may show complete penetration in the host shell (often another brachiopod); these scars or holes (common in the Paleozoic) could be confused with those of other, unknown, Paleozoic borers.

Within the Prosobranchia, there are two major groups of shell boring (or drilling) predators, the Naticidae (Mesogastropoda) and the Muricidae (Neogastropoda). I have summarized only a small part of the extensive research on muricid predation, and have limited it to the principal means of distinguishing their predation from naticid predation. A comprehensive review of muricid predation will be most useful but remains to be written.

An heuristic definition of gastropod boreholes was provided by Carriker & Yochelson (1968: 2) as "an excavation of characteristic size and form drilled by a predatory snail in the calcareous exoskeleton of a prey organism by means of chemical weakening and radular abrasion of the prey shell for the purposes of obtaining food." Refinements of this definition were provided by Chatterton & Whitehead (1987: 68). Specifically, naticid boreholes are parabolic holes (straight or oblique), formally referred to as a "truncated spherical paraboloid"; the borehole is countersunk (i.e., the enlarged outer margin is beveled or tapered, forming a chamfer) (Fig. 1), and incomplete naticid boreholes are characterized by a prominent central boss (rounded elevation) on the bottom surface (Fig. 2).

The Muricoidea (Neogastropoda) is a diverse group containing a variety of eclectic predators, including shell borers, carrion feeders, and other specialized predators, as well as several herbivores. The majority of muricids are shell borers and are distinguished by the presence of the accessory boring organ (ABO) in the sole of the foot. The muricid borehole is cylindrical, with nearly straight edges (Fig. 3); the naticid borehole, in contrast, has a more parabolic form and beveled edges. Much of the research carried out on the oyster drill, *Urosalpinx cinerea,* and other shellish pests by Carriker, along with research on other muricoideans by Taylor, has greatly added to our knowledge of the feeding biology of this superfamily (Carriker, 1981; Taylor et al., 1980).

The Nassariidae, or mudsnails, are carnivorous or scavenging members of the Neogastropoda. Fischer (1962a: 75) and Reyment (1966: 34) stated in passing that nassariids are shell borers. Subsequently, Ilina (1987: 23) also mentioned that they probably are shell borers. This appears to be mistaken, as no documentation has ever been provided for boring by mudsnails. Similarly, Stevanovic (1950) thought that the boreholes in mollusks from the Serbian Upper Miocene were caused by the hydrobiid gastropod *Sandria* [= *Pseudamnicola*] *atava;* Ilina (1987: 25) rejected this conclusion and attributed the boreholes to the naticid *Euspira helicina.*

The Cassidae (Tonnoidea, Mesogastropoda) are important predators of tropical echinoids, using sulfuric acid from their proboscis gland along with the radula to penetrate the echinoid test (by cutting out a disc, rather than drilling a hole) (Fig. 4). Hughes & Hughes (1981) provided a comprehensive review of the biology and ecology of cassid predation, and pointed out that other tonnoideans which feed on mollusks do so without boring (i.e., by penetrating between the gastropod operculum and shell, or between the valves of a clam). The numerous unique aspects of cassid predation clearly suggest an independent origin from that of naticids or muricids. Tertiary echinoids with cassid holes were documented by Sohl (1969: figs. 7–8) and Beu et al. (1972).

The Capulidae (Mesogastropoda) are specialized ectoparasitic symbionts of mollusks and echinoderms. They are known to drill holes into the shell of their mollusk host for the purpose of obtaining small amounts of fluids from the host's feeding current for nutrition. Matsukuma (1978) reviewed shell boring by capulids and recorded several fossil records of capulid boreholes: these are sharp-sided cylindrical holes, similar to those produced by muricids. However, capulid boreholes can be recognized by the surrounding attachment scar on the host shell, where the edge of the capulid shell had slightly worn away the host shell (Figs. 5, 6).

In the Opisthobranchia, the nudibranch *Okadaia elegans* (Vayssiereidae) is known to drill holes into the calcareous tubes of serpulid and spirorbid polychaete annelids (Young, 1969). These minute bore holes (Figs. 7, 8) are similar in shape to those of muricids; however, muricids are not known to prey on these polychaetes, whereas *Okadaia* does not feed on mollusks.

In the Pulmonata, the terrestrial *Aegopinella* (Zonitidae) are known as shell-boring predators of other gastropods. Mordan (1977: 65) described predation by *A. nitidula,* in which prey snails (typically other zonitids) are first attacked through the aperture (followed by consumption of the head-foot); subsequently, a quite irregular hole on the umbilical surface of the last whorl is bored (Fig. 11), allowing the predator access to the rest of the prey flesh. Pulmonate shell boring may have evolved from simple shell "radulation," or the scraping of the outer surface of prey shells (Mordan, 1977: 70–1).

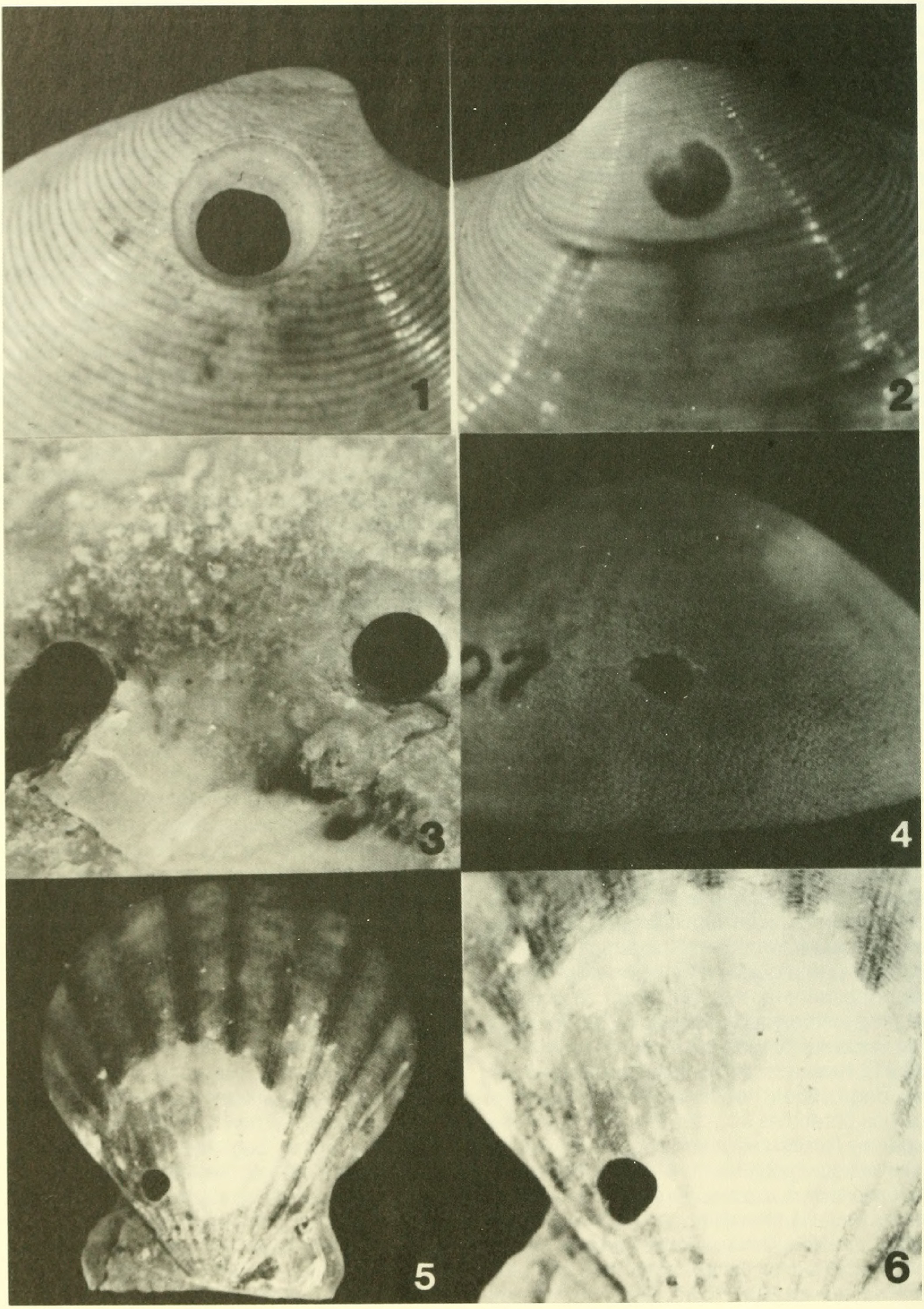
In the Cephalopoda, the octopuses are shell boring predators of a variety of marine shelled mollusks (Ambrose, 1986; Nixon & Maconnachie, 1988). Octopus boreholes can be recognized by their distinctly irregular or oval (but not circular) outline and their extremely small inner borehole diameter, in contrast to the large outer borehole diameter (Ambrose et al., 1988) (Fig. 9). Furthermore, the purpose of the hole is solely for the injection of venom to relax or kill the prey, which is then extracted through the aperture or valve opening. One problem with the analysis of octopus predation is that octopuses frequently break open the shell or otherwise capture the prey without drilling the shell (Ambrose, 1986: table 1). Hence, octopus boreholes represent only part of their trophic activities. Probable octopus boreholes from the Pliocene were reported by Robba & Ostinelli (1975: 338–344).

An unusual polyclad turbellarian flatworm, *Pseudstylochus ostreophagus,* is known to bore a hole in the shell of juvenile oysters (spat), effecting separation (or relaxation) of the prey adductor muscle, which causes the shell valves to gape, facilitating entry of the predator between the valves leading to prey consumption. The irregular oval holes are quite small (typically 150 × 190 μm); further details are provided by Woelke (1957). Many polyclads are known predators of mollusks, but shell boring has not been shown for other species (Galleni et al., 1980: table 1).

Nematode worms are known to prey upon the microscopic Foraminifera (Granuloreticulosa), boring one or more holes in the test, entering the chamber, and slowly consuming the prey. In the past, such holes were thought to be produced by juvenile gastropods (Livan, 1937: 149; Saïdova & Beklemishev, 1953; but see Fischer, 1962a: 70–1); however, their size (less than 60 μm in diameter) is smaller than those produced by newly hatched predatory gastropods (boreholes 100–160 μm in diameter). Sliter (1971) found that nematodes were responsible for this predation, and illustrated the various borehole morphologies (irregular oval to bevelled round). Subsequently, Arnold et al. (1985) described even larger boreholes (10–125 μm in diameter) in Foraminifera from the Galápagos hydrothermal vent mounds, and concluded that naticid gastropods were probably responsible (despite the fact that naticids are not known from such habitats). These are also likely to be the product of nematodes.

Decapod crustacean predation on mollusks is well known, and typically takes the form of shell breaking or cracking followed by extraction of the prey. Occasionally, the prey is able to escape and repair the broken shell, leaving diagnostic shell repair scars (Fig. 10) as a sign of unsuccessful predation (Schäfer, 1972: 408–411; Vale & Rex, 1988). Usually, the shell is fragmented; in a few cases, the predator may only effect a smaller, very irregular hole in the otherwise intact prey shell. Papp et al. (1947), provided an extensive discussion of crab predation; subsequent authors have documented the presence of shell fragments or subsequent shell repair attributable to predation attempts (successful and unsuccessful, respectively) by crabs and other decapods. However, because of fragmentation, one cannot account for all the remains of such predation. Shell fragmentation may also occur because of wave action; Cadée (1968: 87–88) noted that this is usually accompanied by signs of abrasion and fragmentation in subtidal shells is probably restricted to predation.

A most novel recent discovery is that of Norton (1988) who documented holes made in gastropod shells by a marine cottid fish, *Asemichthys taylori*. This species has a special set of vomeral teeth that are used to punch a hole or series of holes in the prey



FIGS. 1–6.

shell (Fig. 12). The holes (which are not truly "bored") allow the entry of digestive enzymes while the shell is in the digestive tract of the fish. Shells which are unpunched generally pass through undigested and emerge alive (except, of course, for limpets which have an exposed ventral aspect). Similar rows of punctures in Paleozoic brachiopods, conulariids and nautiloids were attributed to shark predation (Mapes et al., 1989, and references therein).

Shell boring or burrowing is little known in the freshwater environment, with a few exceptions, such as the endolithic burrowing polychaete *Caobangia* (Jones, 1969). Recently, the Soviet paleontologist Ilina (1987) found shells of *Unio* and *Viviparus* (freshwater mollusks) with regular, round boreholes, one to four per shell, with an outer diameter up to 2 mm and an inner diameter from 1.0 to 1.5 mm. Ilina (1987: 29) suggested that these holes were made by ". . . ants that for reasons not yet known use their formic acid to etch perforations in the shells of molluscs . . ."; E. O. Wilson (*in litt.*) stated that "I don't know of any documented cases of ants boring mollusk shells, and I doubt very much if they do . . . it's hard to imagine their cutting through a clam shell even with the aid of formic acid." In any case, since ants are terrestrial, it seems unlikely that these freshwater mollusks were drilled and consumed *in situ;* it is more likely that empty shells were washed ashore and (post-mortem) excavated by some other organism, perhaps for a refuge. Further study is clearly indicated.

Finally, there is an extensive and scattered literature on shell borings in Paleozoic fossils. While providing lengthy descriptions of the bore holes and of the prey organisms, these studies generally have not elucidated the nature of the predator (known predatory gastropods did not evolve until the Mesozoic). Carriker & Yochelson (1968) suggested that these holes were made by soft-bodied, sessile, non-predatory organisms of unknown taxonomic affinity (this hypothesis is essentially non-testable!); Sohl (1969: 728–9) further discussed this problem. More recently, Smith et al. (1985) and Chatterton & Whitehead (1987) reviewed the Paleozoic boreholes and suggested that they were, indeed, predatory in origin although the identity of the predator remains unknown. Vermeij (1987: 176–7) hypothesized that ectoparasitic platyceratid gastropods (ecologically analogous to capulids) were the Paleozoic borers.

The remainder of this paper is restricted to analysis of predation by naticids. The preceding review of the diversity of shell borers indicates that predation by boring has evolved independently in a number of taxa; any similarities are undoubtedly cases of convergent evolution. The following section, on the proximate mechanisms, demonstrates the numerous unique (derived) aspects of naticid predation, and should be compared with what is known for other shell-boring taxa.

MECHANISMS OF NATICID PREDATION

For a detailed review and critique of the previous morphological studies on naticid feeding mechanisms, see Carriker (1981). Essentially, early controversies concerning naticid boring involved the means of boring: i.e., was it solely by mechanical means (radular rasping of the prey shell) or did it also involve chemical action (acid secretion). It was the careful work of Carriker and colleagues (Carriker, 1981) which demonstrated that the latter hypothesis is the case for naticids and muricids.

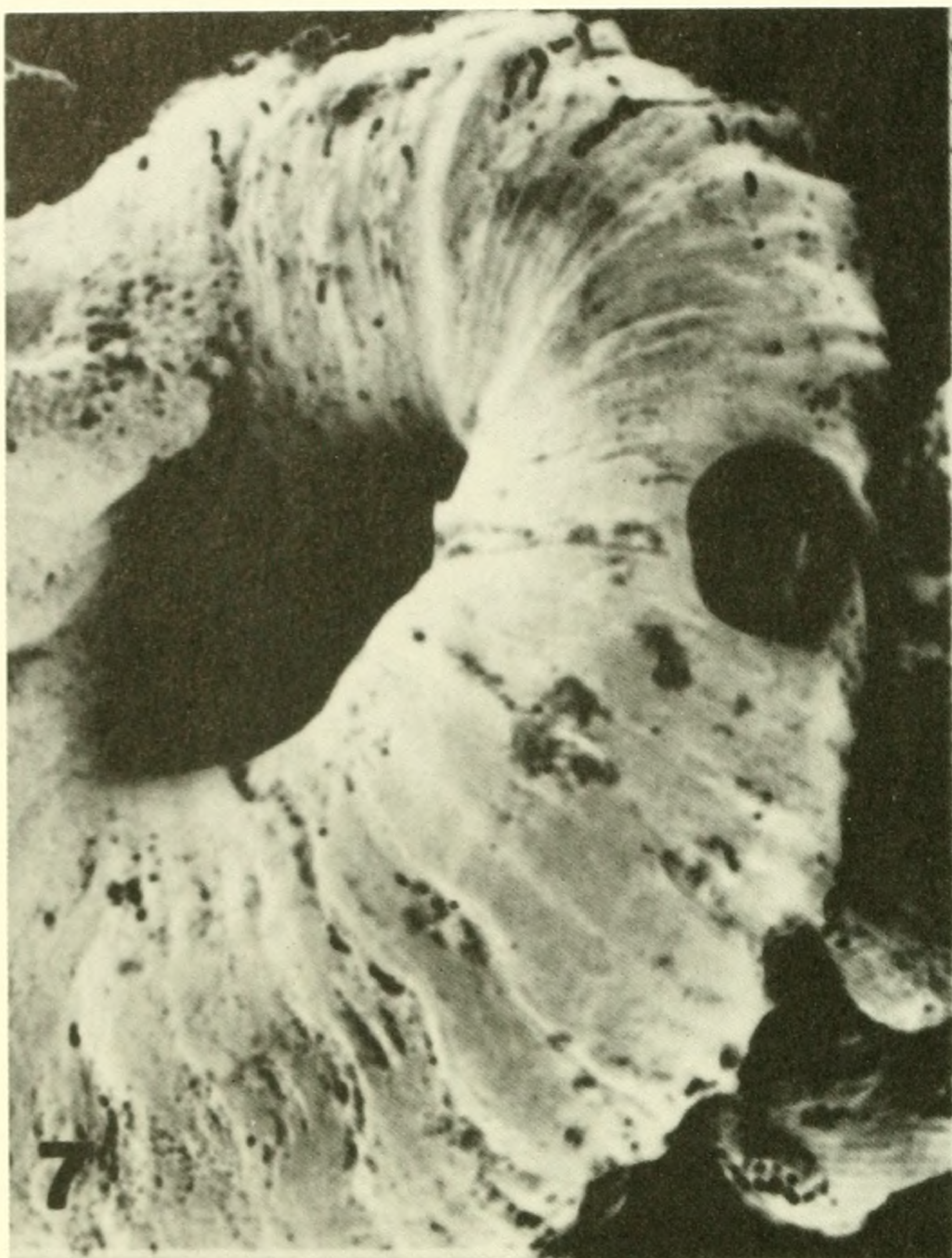
FIG. 1. Naticid bore hole (complete) in valve of *Dosinia discus* (Reeve, 1850) [Cocoa Beach, Florida; MCZ 145801]. Shell dimensions 52.7 mm × 48.8 mm; outer bore hole diameter 5.2 mm; inner borehole diameter 2.8 mm.

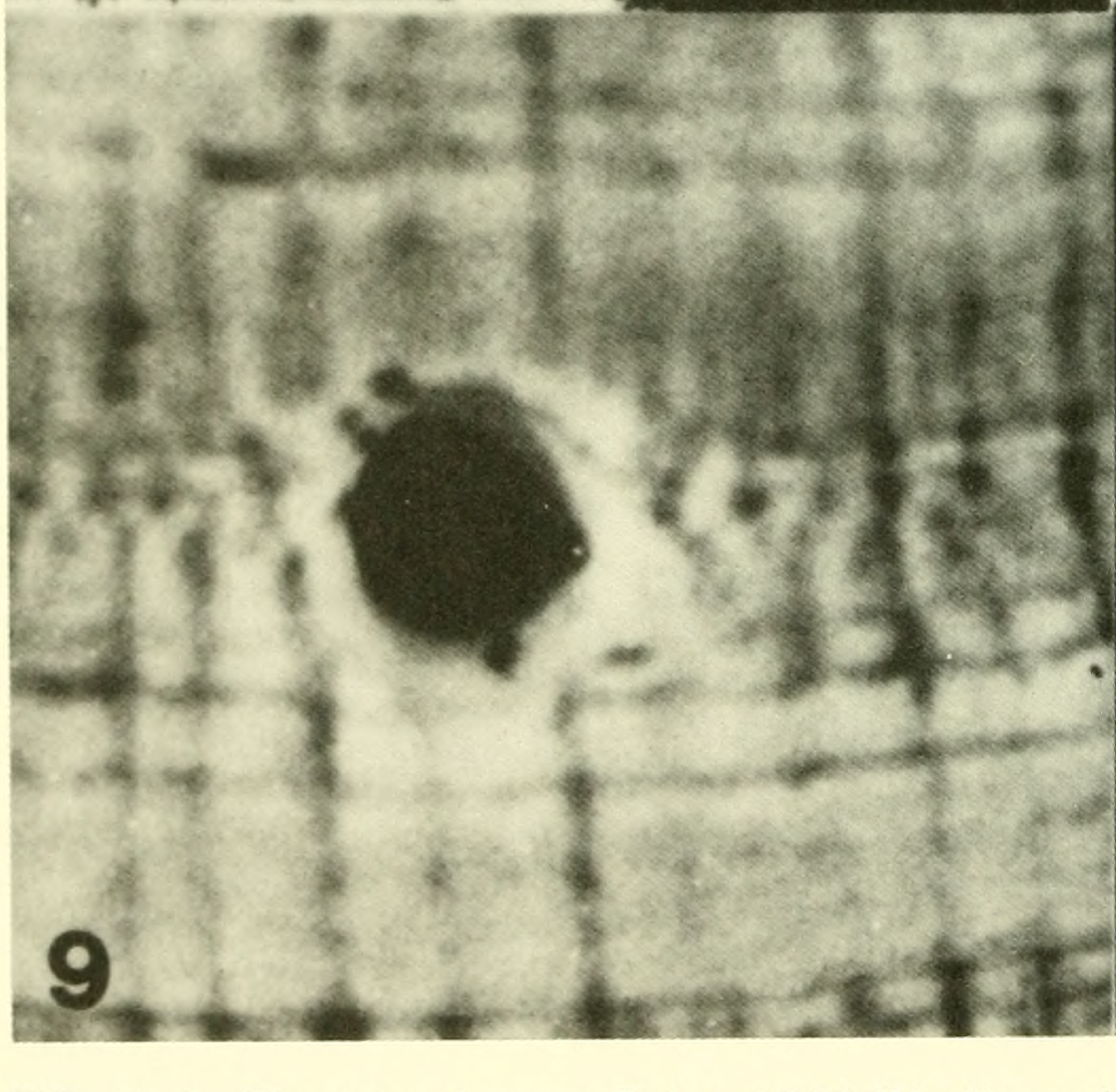
FIG. 2. Naticid bore hole (incomplete) in valve of *Dosinia concentrica* (Born, 1778) [Punta Guanajibo, Puerto Rico; MCZ 212607]. Shell dimensions 55.7 mm × 52.3 mm; outer bore hole diameter 2.7 mm.

FIG. 3. Muricid bore holes [presumably by *Urosalpinx* or *Eupleura*] in adjacent valves of *Crassostrea virginica* (Gmelin, 1791) [Stono River, South Carolina; MCZ 226338]. Shell lengths 86 mm and 65 mm; outer bore hole diameter 2.5 mm; inner bore hole diameter 2.3 mm.

FIG. 4. Cassid bore hole in *Cassidulus pacificus* (A. Agassiz, 1863) [Punta Pescadero, Baja California Sur, Mexico; USNM 32907]. Test dimensions 34.9 mm × 28.9 mm, height 16.1 mm; bore hole diameter 2.1 mm.

FIG. 5, 6. *Capulus danieli* (Crosse, 1858) bore hole in valve of *Comptopallium vexillum* (Reeve, 1853) [Noumea, New Caledonia; ANSP 272383]. Scallop shell dimensions 32.5 mm × 29.5 mm; outer bore hole diameter 1.75 mm; capulid shell dimensions 4.9 mm × 15.0 mm.





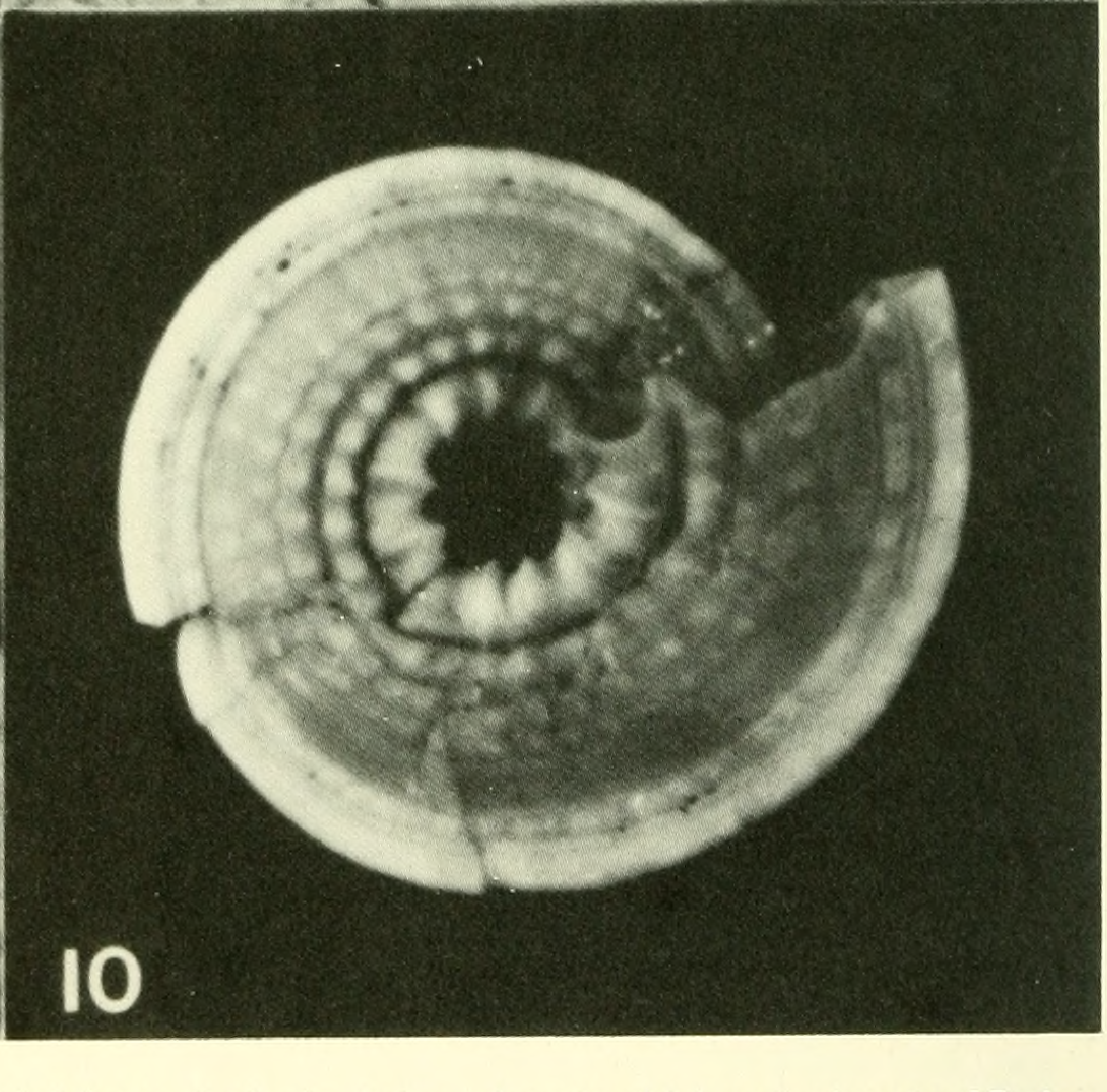


FIG. 7, 8. *Okadaia elegans* Baba, 1930 [Nudibranchia] bore hole in tube of spirorbid polychaete [Oahu, Hawaii]. Bore hole diameter ca. 115 μm; worm tube diameter at bore hole ca. 300 μm. SEM photographs courtesy J. D. Taylor. [Magnifications; Figure 7 at 110×; Figure 8 at 350×].

FIG. 9. *Octopus bimaculatus* Verrill, 1883 bore hole in *Ventricolaria fordi* (Yates, 1890) [Anacapa Island, off Ventura, California; MCZ 298337]. Shell dimensions 33.7 mm × 31.2 mm; outer bore hole diameter 2.2 mm, inner bore hole diameter 0.6 mm. Specimen courtesy R. F. Ambrose.

FIG. 10. Unsuccessful crustacean predation: shell repair scars in *Architectonica nobilis* Röding, 1798 [Puerto Plata, Dominican Republic; MCZ 106825]. Shell dimensions 8.8 mm × 17.5 mm.

A fundamental and little studied problem concerns the methods by which naticids detect their prey. For many predatory gastropods, chemoreception (detection of prey "chemical odors" by the osphradium) is typically the initial mechanism for determining the presence and direction of potential prey (Kohn, 1961; Croll, 1983). With infaunal naticids, the sediment habitat not only decreases the diffusion rate of chemical substances, but also may perturb its directionality; hence naticids may forage with the siphon extending to the surface where diffusion is more direct and rapid. Kitching & Pearson (1981) found that the Australian "*Polinices*" [= *Conuber*] *incei* responded to artificial sound waves directed through the substrate, which presumably mimicked the vibration of burrowing prey. Mechanoreception may well serve as an additional prey detection mechanism for the naticids.

Regardless of how the prey are initially detected, one can analyze the behavioral perspective: namely, recognition of suitable prey serves as a releasing mechanism which elicits a stereotyped sequence of behaviors [= fixed action patterns] (Ansell, 1960). Naticids have been little studied with respect to classical ethological principles, probably because most activity occurs while they are buried.

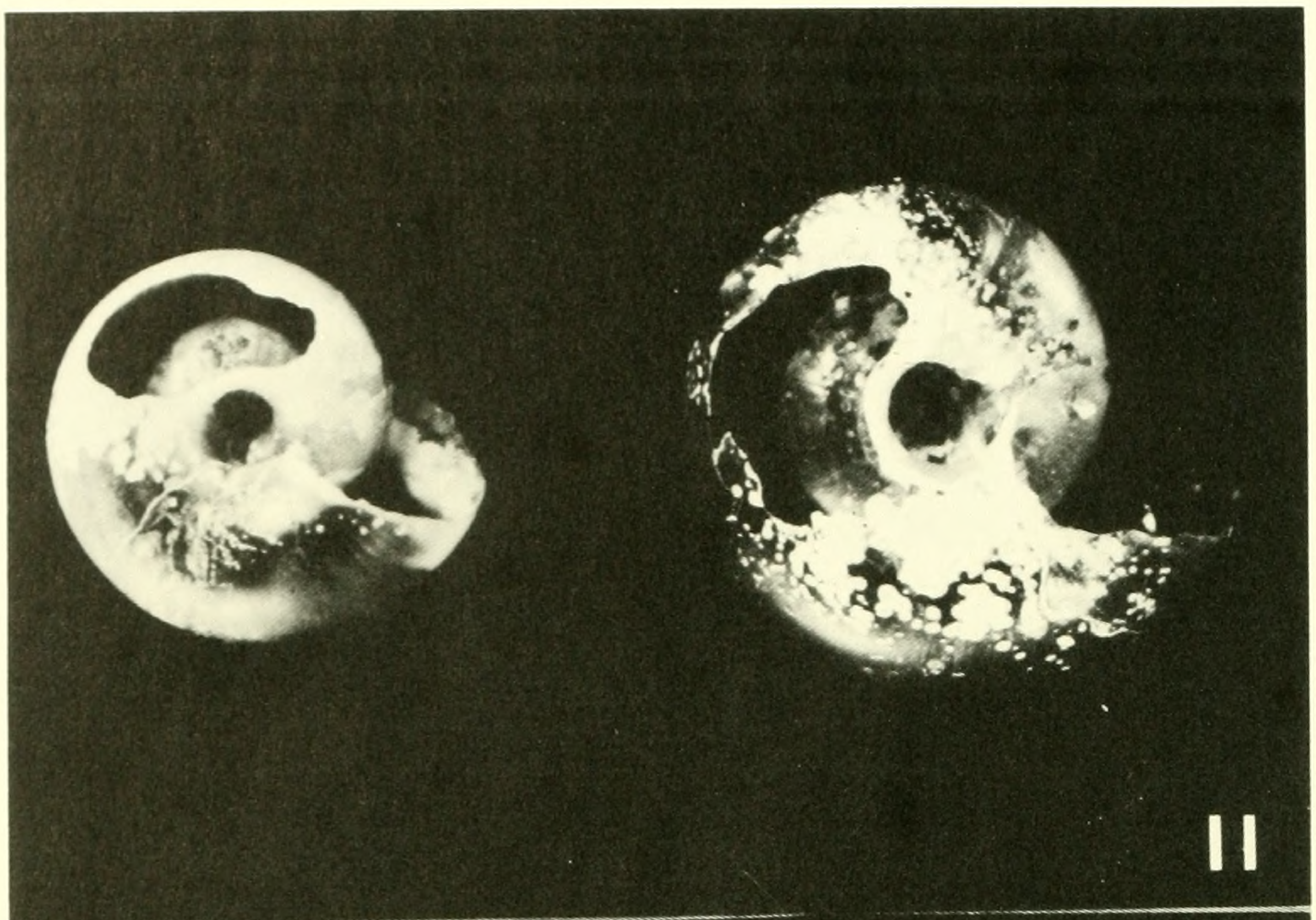
Edwards (1969), Schäfer (1972: 242–3), Stenzler & Atema (1977) and Hughes (1985) discussed the sequence of prey capture events: the prey is detected, evaluated, seized, covered and immobilized with copious pedal mucus, wrapped in the dilated foot of the naticid, dragged for some distance, and finally carried deep into the sand for commencement of boring.

The mechanism of naticid boring involves a complex sequence of events. There is alternate application of the predator's radula and accessory boring organ (ABO) to the bore hole site on the prey shell. The ABO is found on the ventral surface of the proboscis in naticids (but in the sole of the muricid foot); the two ABO types represent a case of convergent evolution and no homologues in other taxa are known. The ABO histology was described by Bernard & Bagshaw (1969), who characterized it as a "fungiform papilla" containing numerous epithelial secretory cells. The biochemistry of ABO secretions was discussed by Carriker & Williams (1978). The ABO secretes a complex mixture of presumed enzymes, chelators, and inorganic acid (HCl) in a saline, hypertonic solution which effects dissolution of the prey shell layers (both calcareous and organic matrix). During boring, the proboscis becomes engorged, everting both the radula and the ABO. The radula is protracted and scrapes at the surface of the bore hole. The proboscis is rotated in 90° sectors and the scraping is from the outer edge to the center, resulting in the diagnostic boss in the center of incomplete bore holes (Ziegelmeier, 1954: fig. 7; Carriker, 1981: 410). The prey shell fragments are ingested but subsequently excreted without digestion (Carriker, 1981: 411). The prey tissue is ingested by the proboscis through the borehole; Reid & Gustafson (1989) determined that external digestion does not occur.

Most studies have documented that naticids capture and consume their prey entirely within the sediment. Previous reports of naticid predation on the sediment surface were usually a result of aquaria studies wherein the sediment depth was too shallow and consequently abnormal behavior patterns were manifested. Recently, field observations of *Natica gualteriana* from the Philippines (Savazzi & Reyment, 1989) have documented that this species was capable of searching for and capturing its prey on sand bars at low tide (i.e., while exposed to the air). Further study is needed to ascertain whether other naticid species can also feed on the sediment surface (exposed or subtidally). As such, this would result in greater competitive interactions between those naticids and the epifaunal muricids.

For temperate and boreal naticids, the water temperature can determine the active periods of feeding. Hanks (1953) showed that the northwest Atlantic *Neverita duplicata* and *Euspira heros* had a marked temperature-dependence, with no feeding at temperatures below 5°C and 2°C, respectively. Similarly, salinity (brackish or estuarine waters) also affects feeding rates; these two naticid species did not feed at artificial salinities below 10‰ (normal seawater about 35‰).

For the calculation of energy budgets, the rates of shell boring and of prey tissue ingestion must be determined. Determining the time for infaunal prey capture and subjugation would be extremely difficult and yields variable results (here, especially, aquaria studies would be of little value). In general, the relative sizes of predator and prey (both dimensional and shell thickness) must be taken into account; there will undoubtedly be great interspecific variation in these rates. Ziegelmeier (1954) found a boring rate of 0.6 mm/day, or 0.025 mm/hour by *Euspira nitida*. Similarly, Kitchell et al. (1981: fig. 2) observed that in *Neverita duplicata* preying on various bivalves, the boring rate was a nearly constant 0.0223 mm/hour, regardless of prey species, predator size, or elapsed time. Bayliss (1986) noted that for *Mya* and *Spisula* prey, *Euspira*



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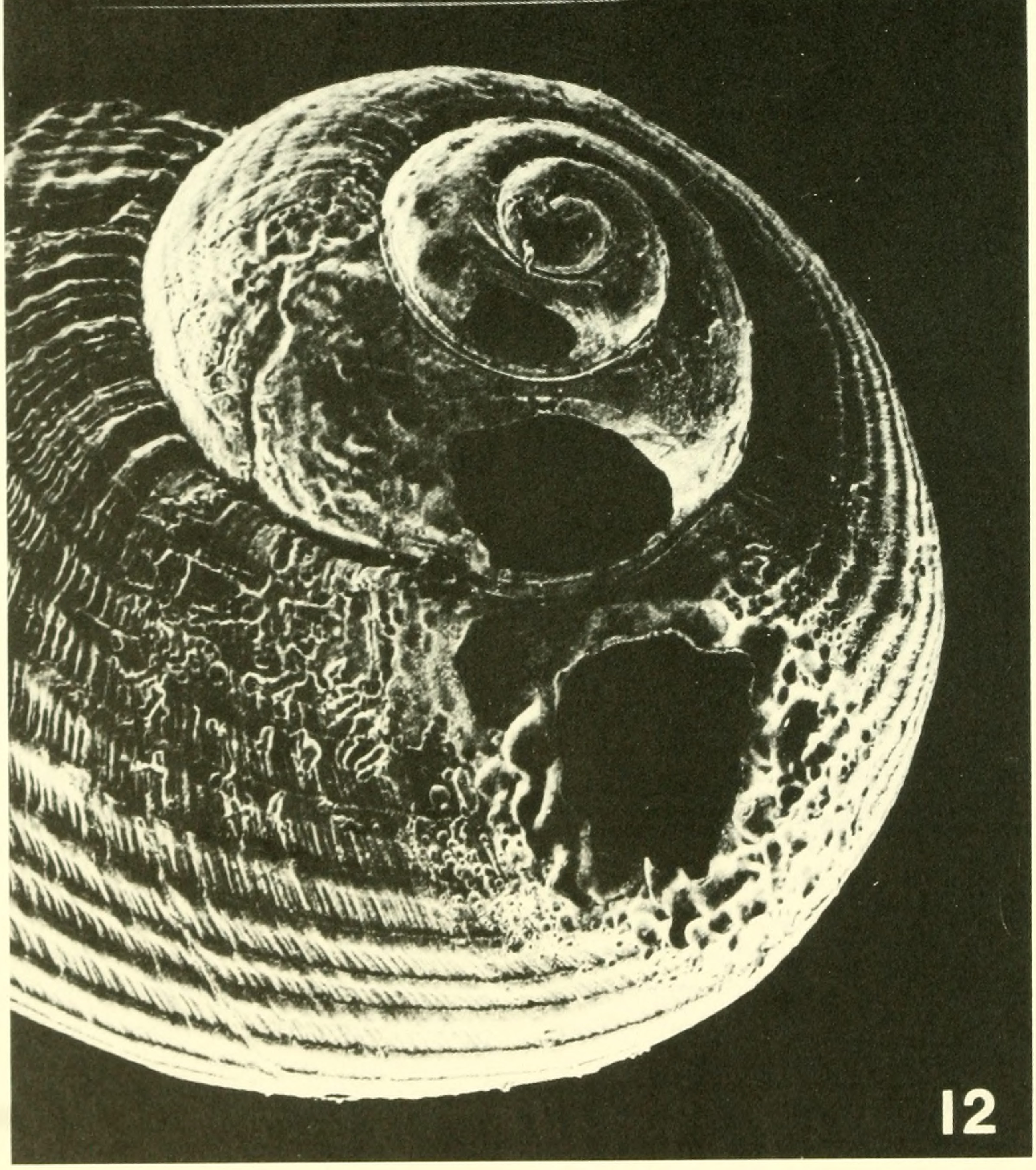

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FIGS. 11, 12.

alderi bored at an average rate of 0.0097 mm per hour; the prey tissue was consumed in 19.5 hours (*M. arenaria*), 21.5 hours (*S. subtruncata*), or 60 hours (*S. elliptica*).

For the analysis of naticid boring predation, especially in fossils, the primary source of data for the predator is the size of the borehole. Kitchell et al. (1981: 539, fig. 4) proved that the borehole diameter is constant for a given predator size, regardless of the prey size. Most studies have used the inner borehole diameter as the basis for analysis, as this represents the size of the predator's proboscis. Wiltse (1980a: 189, fig. 1) used the diameter ". . . at the junction of the prismatic and nacreous shell layers"; this does not facilitate comparisons with other prey taxa (given that the depth of this junction is not constant for all taxa). Usually, the outer borehole diameter is also directly proportional to the predator size; but due to the chamfered borehole edge, it is more difficult to measure. However, for corbulid bivalve prey, there is an exception in that the outer borehole is disproportionately much larger than the inner borehole; this reflects the conchiolin layer in the prey shell (De Cauwer, 1985). Arua & Hoque (1989b), based solely on analysis of outer borehole sizes, concluded that the opening was more oval than circular; regrettably, their data on inner borehole sizes was not presented.

It is unfortunate that a recent paleoecological study (Arua & Hoque, 1989a, 1989c) seems to have confused several muricid boreholes with those of naticids, and *vice versa.* Their "hole types" A, B and D were claimed to be muricid; C, E and F as naticid. The authors had stated that naticid boreholes are countersunk, with tapering sides, and incomplete ones have a central boss; yet, they claimed that their "hole type E," which lacks a boss and has vertical sides, was naticid! My re-analysis of their descriptions leads to the conclusion that their "hole types" E and (maybe) A are muricid; whereas B, C, D, and F are naticid. This confusion undoubtedly has arisen in other studies, and should be considered when interpreting community-level analyses (because the variety of observed boreholes are rarely illustrated therein).

A more general aspect of naticid predation is the suitability of the substrate for naticid locomotion. It is well known that naticids are restricted to infaunal sedimentary habitats; it is less appreciated that extremely fine or smooth grained substrates (silt-mud-clay) are precluded because they are too tightly packed to burrow through readily, in contrast to coarser sand substrates (Yochelson et al., 1983: 12; Maxwell, 1988: 31).

Vermeij (1980) and Ansell & Morton (1987) discovered that the tropical *Polinices "tumidus" [= mammilla],* after wrapping its prey in a mucus coat within the foot, retained the prey until suffocation and gaping occurred. Subsequently, the prey was consumed without boring. Ansell & Morton (1987: 117) suggested that a "narcotizing toxin" may play a role in causing prey gaping, such as by thaidine gastropods preying on barnacles. This was questioned by Reid & Gustafson (1989), who determined that prey suffocation alone caused shell gaping. The ecological and evolutionary implications of this non-boring predation will be discussed below.

A preposterous view of the evolution of naticid feeding mechanisms was advanced by Stafford (1988), who claimed that naticids originated at Ediacaran-Cambrian times (570 million years ago), as swimming filter feeders, and gradually shifted to benthic feeding entailing eversion of the stomach (as in asteroids) to effect external digestion of the prey.

To summarize the proximate mechanisms of naticid shell boring: (a) Prey are detected by chemoreception using the osphradium, though mechanoreception may also play a role. (b) Suitable prey are seized, covered with pedal mucus and wrapped in the foot. (c) The proboscoideal acid-enzyme secretory accessory boring organ (ABO) together with the radula is used to excavate a countersunk (bevelled) hole in the prey shell, and the prey tissues are extracted through this borehole. The size of the borehole (inner diameter) is

FIG. 11. *Aegopinella nitidula* (Draparnaud, 1805) [Zonitidae] bore holes in (left) *A. pura* (Alder, 1830) [bore hole 1.5 mm × 0.7 mm] and (right) *A. nitidula* [bore hole 1.6 mm × 1.0 mm] [Monks Wood, England]. Photographic negative courtesy P. B. Mordan; original in the *Biological Journal of the Linnean Society* (1977), 9: 65, plate 1A. [Copyright 1977 by The Linnean Society of London].

FIG. 12. *Asemichthys taylori* Gilbert, 1912 [Pisces], punched holes in *Margarita* sp. [San Juan Island, Washington]. Shell width ca. 2 mm. Maximum hole diameters: 165 μm; 350 μm; 380 μm. SEM negative courtesy S. F. Norton; original in *Science* (1988), 241(1): cover. [Copyright 1988 by the AAAS].

positively correlated with predator size. (d) Some tropical Indo-Pacific naticids are able to immobilize their bivalve prey until shell gaping occurs, allowing direct access to the prey tissues; thus, no borehole need be made.

THE PREY OF NATICIDS

The Appendix tabulates the known prey of naticid gastropods (fossil and Recent). The genera are arranged alphabetically by family; the reference is given in brackets following the species name [*n.b.* this is not the author of the taxon!]; some species were reported in several studies but only one such is indicated herein. This compilation includes an unpublished data set on Fijian Pleistocene mollusks collected by A. J. Kohn. I have corrected for obvious changes in generic nomenclature; species names were not given for several reports, as indicated by an asterisk. Many records of naticid predation are purely incidental or even parenthetical (e.g., "by the way, some of the shells of X were bored . . ."), which does not facilitate critical comparative analyses.

Generally, the records herein are limited to ecological or paleoecological studies emphasizing predation; it is too time-consuming to search through the general systematic and faunistic literature for scattered records of naticid predation (which are usually not thoroughly documented in such papers). Needless to say, aquarium studies of naticid feeding should be based on prey found in the same habitat as naticids. Unfortunately, some papers (Hayasaka, 1933; Fischer, 1966; Sander & Lalli, 1982; and De Cauwer, 1985) provided lists of taxa with gastropod boreholes, but without specifying naticid or muricid boreholes. Nonetheless, based on the available data, it appears that naticids prey on the majority of benthic, infaunal shelled mollusks.

A. Class Gastropoda

Since most archaeogastropods (e.g. Pleurotomaroidea, Fissurelloidea and Patelloidea) are rocky-habitat dwellers, they are not subject to naticid predation. Beebe (1932: 212, fig.) made the unusual statement that, in Bermuda, *Natica canrena* preyed upon the rocky intertidal limpet *Fissurella barbadensis,* leaving a diagnostic borehole in the limpet shell. My subsequent re-analysis of this situation reveals that Beebe had confounded the excurrent slit or foramen ("keyhole") of these limpets with naticid boreholes and erroneously assumed that naticid predation was responsible for the limpet keyholes!

Many of the soft-substrate taxa in the Mesogastropoda are subject to naticid predation. Not included herein are the extensive reports of confamilial predation on naticids themselves (sometimes referred to as "cannibalism") (Kabat & Kohn, 1986). Reports of naticid boreholes in *Xenophora* [Xenophoridae] and *Lamellaria* [Lamellariidae] by Adegoke & Tevesz (1974) are questionable, given the epifaunal habitat of these taxa. While it may appear that neogastropod genera are more frequent in the list, this could be a taxonomic artifact of generic lumping *vs.* splitting.

Most of the neogastropods are active predators themselves; the epifaunal and rocky-habitat species generally escape naticid predation. It is entirely possible that some of these records, especially of Muricidae, are of misidentified muricid boreholes.

B. Class Bivalvia

Most infaunal bivalves are subject to naticid predation. In particular, the venerids, tellinids, and lucinids (the last two often with relatively thin or little-sculptured shells) are frequent victims. The infaunal Solemyidae live in reducing sediments where naticids are not found. Bivalve taxa that are in rocky habitats, epifaunal byssate or cemented (Dimyoidea, Plicatuloidea, Anomioidea, Chamoidea, Leptonoidea and Cyamioidea) effectively escape naticid predation; the few cases of naticid boreholes in the Pterioidea, Limoidea, Ostreoidea and Pectinoidea are unusual exceptions. Those that are rock or wood burrowers (Lithophagidae, Gastrochaenoidea and Pholadoidea) are also inaccessible to naticids. The Pinnoidea and Tridacnoidea have encrusted and sculptured shells; the Glossoidea, Clavagelloidea and Pholadomyoidea are too rare to have been reported in this context.

C. Class Scaphopoda

A thorough review of naticid predation on scaphopods by Yochelson et al. (1983) found that scaphopods were the occasional prey of naticids from the Late Cretaceous to the Recent. Usually, there is moderate stereotypy of borehole siting, with most being laterodorsal and about midway along the shell axis. It was found that coarse-ribbed scaphopods (which live in coarse sediments) were much more likely to be bored; those with smooth (or no) ribs, living in fine sediments, escaped naticid predation by virtue of their habitat which is inimical to active naticid burrowing (Yochelson et al., 1983).

D. Other Mollusk classes

Naticid predation has not been recorded on the Aplacophora, Monoplacophora, Polyplacophora, or the Cephalopoda. The shell-less Aplacophora would not leave traces of naticid predation. The Monoplacophora (clay-mud habitats) and the Polyplacophora (rocky habitats) are usually not encountered by naticids. The epifaunal and pelagic cephalopods, predators themselves, are unlikely to be captured by the slower naticids.

E. Polychaetes

Paine (1963: 69) found one specimen of *Neverita duplicata* from Florida that fed on the polychaete *Owenia fusiformis;* this is the only known record of naticids preying on annelids. It is not clear whether this represents normal behavior or a single, aberrant event.

F. Crustaceans

Significantly, Gonor (1965: 229) found that naticids would not feed on hermit crab occupied shells. This is of importance as it indicates that not only can naticids recognize such "prey" (of course, the active epibenthal hermit crabs may be beyond the range of naticids), but also that boreholes found in shells with recognizable signs of hermit crab occupancy (worn lips, unrepaired damage, epibionts) were the cause of the gastropod mortality, freeing the shell for hermit crab use.

Ostracods represent a potentially important prey source for juvenile naticids. Livan (1937) and Reyment (1966, 1967) attributed numerous boreholes in ostracods to predatory gastropods. Maddocks (1988) reviewed the various types of boreholes in ostracods (Cretaceous to Holocene of Texas) and concluded that juvenile naticids were responsible for most. However, because of the thin ostracod test, there is a wide variety of "holes" and it is difficult to attribute them to known causes (Reyment et al., 1987).

G. Brachiopods

Most articulate brachiopods live in rocky habitats (rock walls or boulder grounds), thereby escaping naticid predation because of habitat incompatibility. However, Witman & Cooper (1983: 71, figs. 8c–d) reported "naticid" boreholes in values of *Terebratulina septentrionalis* from the Gulf of Maine, which they attributed to either *Natica clausa* or *N. pusilla.* The illustrated boreholes resemble those of muricids (albeit with slightly sloping sides); further study is recommended.

H. Pisces

Perry (1940: 116) reported that the tropical western Atlantic *Naticarius canrena* "preys on bivalves and has been seen to devour dead fish." This remarkable observation, if true, represents the only known record of piscivory in the Naticidae. However, if it is based on aquarium observations, then it may simply reflect aberrant behavior by starved individuals (see the next paragraph).

I. Scavenging

Most studies have shown that naticids will only feed on fresh prey; carrion-feeding (as in the neogastropod Buccinidae and Nassariidae) is not manifested. A few studies (typically in aquaria) have shown that gaping (dying) bivalve prey may be consumed directly without boring (Ansell & Morton, 1985). It is not clear if this laboratory behavior is also shown in the field.

J. Egg Capsules

Several authors have reported "naticid" boreholes in the egg capsules of various deep-sea organisms. These observations include Thorson (1935: 12–13, figs. 4a–c) in egg capsules of the neogastropod buccinid *Sipho* [= *Colus*] *curtus* from East Greenland; Jensen (1951, fig. 1) in egg capsules of the ray (*Raia*) from Davis Strait (the boreholes ranged from 0.75 to 2.5 mm in diameter; a few capsules had multiple boreholes); and Ansell (1961) in egg capsules of the dogfish (*Scyliorhinus canicula*) with countersunk boreholes. It must be emphasized that naticids were not observed boring these holes; these authors had merely conjectured that naticids were the most likely causative agents. These boreholes were clearly effected from the outside (i.e., they are not the hatching-out holes of the juveniles within). First, for the buccinid egg capsules, it is probable that a muricid bored the holes, as is known for some other muricids (Abe, 1985). Second, for the elasmobranch egg cases, a more likely predator is the unusual deep-sea archaeogastropod family Choristellidae, which are typically associated with skate egg capsules upon which they feed (Hickman, 1983: 86).

The primary prey sources for naticids are infaunal gastropods and bivalves. The data [Appendix] document that 47 gastropod families (out of 129 shelled marine gastropod families) and 35 bivalve families (out of 109 marine bivalve families) are known to be subject to naticid predation. The major gastropod prey sources are the Turritellidae and Naticidae (Mesogastropoda) and the Turridae (Neogastropoda). The major bivalve prey sources are the Lucinidae, Tellinidae and Veneridae (Heterodonta).

FOSSIL RECORD OF NATICID PREDATION

This section tabulates the reports of fossil naticid predation and is arranged by geological time period. In general, only brief summaries are provided; discussion of any broader ecological aspects is deferred to the following section in combination with related conclusions from Recent studies. It must be emphasized that it is difficult to track down all the paleoecological studies, especially those that are "buried" within lengthy systematic monographs (no attempt has been made to search through the latter). Indeed, it seems better that extensive paleoecological researches should be published separately from narrower taxonomic studies, in order to bring them to wider notice.

A. Triassic

Fürsich & Wendt (1977: 299) mentioned "naticid" boreholes from the Cassian Formation of northern Italy (Tirol). Subsequently, Fürsich & Jablonski (1984) illustrated the boreholes, showing the diagnostic countersunk appearance of incomplete boreholes, and discussed the implications thereof. The bivalve prey were *Cassianella* and *Palaeonucula;* the gastropod predators were referred to several species of the naticid genus "*Ampullina*." Newton (1983; Newton et al., 1987: fig. 25.2) independently documented "naticid" boreholes in the epibyssate limid *Mysidioptera* from the Wallowa Terrane of the Hells Canyon (Oregon-Idaho); this suggests that the Triassic borers were somewhat widespread, before becoming extinct. However, the taxonomy of Triassic "naticids" remains a morass, and their familial assignment is still uncertain. Further discussion of the evolutionary consequences of Triassic boring predation is deferred to the next section. Indeed, if these countersunk Triassic boreholes are **not** those of naticids, then it remains uncertain whether all the younger occurrences of countersunk boreholes are correctly attributed to naticid predation.

Sohl (1969: 726) expressed some doubt as to whether the Triassic forms were true naticids; in any event, his spindle diagram of naticid clade diversity (his fig. 1) clearly shows that from the Triassic to the mid-Cretaceous, there are never more than five genera in any epoch; naticid diversification did not commence until the Upper Cretaceous, with the evolution of the boring habit. Bandel (1988: 270) claimed that "Thus Triassic 'naticids,' to a large extent, are neritoideans, some belong to other groups, but none appear to be naticids"; this needs further documentation.

B. Jurassic

Sohl (1969: 729) searched through various paleontological monographs and collections of Jurassic mollusks and found no signs of molluscan boreholes. Fürsich & Jablonski (1984) also concluded that there were no gastropod borers in the Jurassic.

C. Cretaceous

Fischer (1962a) reviewed some reports of Cretaceous boreholes and attributed most to naticids, as there were relatively few muricids at that time. Subsequently, Sohl (1969: 731) more carefully analyzed Cretaceous boreholes and found a few from the Cenomanian (100 myr) and a much greater abundance from the Campanian (75 myr). The Ripley Formation (Campanian) was studied in greater detail by Vermeij & Dudley (1982) who also found extensive shell repair and a size refuge from boring predation. The oldest Cretaceous records were shifted further back by Taylor et al. (1983) who documented naticid predation from the Blackdown Greensand of

England (Albian, 105 myr). They found that the vast majority (92%) of boreholes were naticid, with a nearly equal ratio of gastropod to bivalve prey (in contrast to the few muricid boreholes, found primarily on bivalve prey). The diversification of naticids (and other modern marine families) at this time represents the "Mesozoic marine revolution" of Vermeij (1977), and is discussed in the next section.

Vermeij & Dudley (1982) reported no predation on naticids in the Ripley Formation (Tennessee); subsequently, Kitchell et al. (1986: 293, fig. 1h) found a multiple-bored specimen of *Euspira rectilabrum,* from the same outcrops. This is the earliest record of confamilial naticid predation in the fossil record.

D. Paleocene

I have not found any paleoecological studies from the Paleocene reporting on naticid boreholes. Naticids were present then; future studies of these faunas would be most worthwhile.

E. Eocene

Fischer (1960, 1962a, 1963) reported on naticid predation in the Lutétien Stage of France and found that for the bivalve *Petunculus* [= *Glycymeris*], 4.6% of the specimens were bored, primarily the smaller ones. For the gastropod *Mesalia,* 70.9% were bored by naticids (of which only 7.7% were incomplete holes), and some had multiple complete or incomplete boreholes. For *Corbula* spp., there was a rather high rate of boring failure (to 26% of the specimens). This fauna was also analysed by Taylor (1970) who found numerous naticid and muricid boreholes and an overall confamilial naticid predation rate of 11.3%.

Siler (1965) briefly reported on the Gosport Formation of Texas and found both naticid and muricid boreholes on the bivalve *Lirodiscus tellinoides.* A more comprehensive study on the Stone City Formation of Texas (Stanton & Nelson, 1980; Stanton et al., 1981) recorded a naticid mortality rate of 15% and a crustacean mortality rate of 20% for molluscan prey. The latter studies entailed considerable efforts to reconstruct the food web and paleocommunity structure.

Several studies were carried out on the Ameki Formation of Nigeria by Adegoke & Tevesz (1974), Arua (1989) and Arua & Hoque (1987, 1989a, 1989c). They found that turrids and terebrids were the preferred gastropod prey; the latter authors also found extensive predation on bivalves. However, as discussed earlier, some of the boreholes seem to have been misidentified (vis á vis naticid *vs.* muricid) by Arua & Hoque. An analysis of bivalve prey (*Arcopsis* and *Limopsis*) from the Pallinup Siltstone in Western Australia found that 9.2% of the bivalves had gastropod boreholes, one fifth naticid and four fifths muricid (Darragh & Kendrick, 1980).

F. Oligocene

Klähn (1932) analyzed naticid predation on other naticids from the Sternberg Formation of Germany and found high predation rates from 53.3% (the second smallest prey size class) to 15%–26% (the other classes); the documentation provided does not facilitate further analysis.

G. Miocene

Hoffman et al. (1974) conducted an extensive study on the Korytnica clays of Poland and found a confamilial naticid predation rate of about 10%; unfortunately, their data (table 1) do not fully partition the boreholes by naticid or muricid sources. Subsequently, Hoffman (1976a) attributed most of the bivalve mortality to sedimentation, rather than predation; similarly, abiotic factors accounted for much of the gastropod mortality (Hoffman, 1976b). Other Miocene outcrops from Poland were studied by Hoffman & Szubzda (1976), primarily with respect to food webs and community structure. Kojumdjieva (1974) studied the Tortonian and Sarmatian outcrops of Bulgaria and found a variety of naticid and muricid prey taxa; very few unsuccessful or multiple boreholes were observed.

Thomas (1976) analyzed naticid predation on glycymerid bivalves from various Neogene (Miocene-Pliocene) outcrops in the eastern United States and concluded that predation rates in the Miocene were comparable to those on Recent glycymerids; however, the size-selectivity data seemed questionable. This research was reanalyzed by Kitchell et al. (1981: 545–548), who determined that the seemingly contradictory results of Thomas could be explained by the fact that there were actually two different naticid predators (of markedly different sizes) in the various fossil faunas; this meant that the observed "changes" in predation intensity or prey size were merely an artifact of which naticid predator was present.

A series of studies on the Chesapeake Group of Maryland was conducted by Kelley (1982a–1989b), with an emphasis on bivalve prey. Nearly three-fourths of the mortality could be attributed to naticid predation; for some prey there was an increase (over geological time) of prey size and shell thickness. This was hypothesized to be an evolutionary response to naticid predation. Dudley & Dudley (1980) made a briefer analysis of boring predation on three mollusk species from these outcrops, and observed a size refuge from predation for the two bivalves studied.

Colbath (1985) reported on the outcrops of the Astoria Formation of Oregon and noted extensive naticid predation, primarily of bivalves; other predation sources were not analyzed. The Wimer Formation of northern California was analyzed by Watkins (1974), who found low levels of naticid predation on several bivalves.

Maxwell provided a thorough systematic and paleoecological analysis of the Stillwater Mudstone of New Zealand and observed considerable naticid predation on various gastropods and bivalves. The data were used to reconstruct food webs (Maxwell, 1988: 34, fig. 3) as part of an overall trophic analysis which also considered non-fossilized aspects of the community. There was extensive confamilial naticid predation, especially of the smaller-sized species. This monograph is an excellent model of integrating systematics with paleocommunity reconstructions.

H. Pliocene

Boekschoten (1967) studied the fauna of the Tielrode Sands of Belgium and reported some confamilial naticid predation, although crustacean predation was a far more important source of mortality for the naticids. The Emporda of Spain was analyzed by Hoffman & Martinell (1984), who observed high selectivity in prey size and borehole site choices. Guerrero & Reyment (1988b) used multivariate analysis to differentiate between naticid and muricid boreholes in *Chlamys* from the Lower Pliocene near Malaga, Spain. Robba & Ostinelli (1975) analyzed gastropod, cephalopod and crustacean predation in the Albenga outcrops of Italy and noted that 13.9% of all specimens were bored, nearly all by naticids. Hingston (1985) reported on the Muddy Creek assemblage from Victoria, Australia, and determined that about 75% of the boreholes were naticid and the remainder muricid; edge drilling of bivalves was rare, and prey shell sculpture resulted in a greater frequency of unsuccessful boreholes.

I. Pleistocene

Kabat & Kohn (1986) analyzed predation on naticids from the Nakasi Beds of Fiji and observed rather high naticid predation rates on *Natica* spp., but considerably lower confamilial predation on species of *Polinices* and *Sinum*. Unsuccessful crustacean predation was quite common; successful crustacean predation probably accounted for a greater amount of mortality than did confamilial predation. Berg & Nishenko (1975) found that 26% of the shells of *Nassarius perpinguis* from the San Pedro deposits of California showed naticid boreholes; stereotypy of borehole siting was shown, although no data on predator or prey sizes were given. A much more detailed analysis of the nearly contemporaneous Puerto Libertad deposits of Sonora, Mexico, and a thorough trophic web reconstruction was conducted by Stump (1975: fig. 18).

J. Sub-Holocene

Yochelson et al. (1983) analyzed naticid predation on scaphopods from the elevated "mud lumps," or diapir structures from the Mississippi River delta (ca. 15,000 years old), and found (in two large samples) that almost 58% of *Dentalium laqueatum* had boreholes. They noted that other scaphopod assemblages (fossil and Recent) showed far fewer naticid boreholes (usually less than 10%); this assemblage undoubtedly reflected exceptional naticid feeding.

Since the end of the Early Cretaceous (Albian), naticid predation has been documented through Holocene faunas (except for the Paleocene), although probable naticids are known from the Jurassic. Potential "naticiform" boreholes from the Triassic are known; the evidence is not conclusive as to whether or not the Triassic predators actually were naticids. The available data do not show any clear trends in the rates of gastropod boring predation since the Cretaceous (Vermeij, 1987: fig. 7.6); however, comparisons between assemblages should be based on ecologically analogous taxa, and studies of a single prey family need to consider possible changes in defense mechanisms (especially shell form) over time.

Another area of interest is the use of bore holes in the field of ichnology, or the study of trace fossils. Most paleontologists recognize animal locomotory tracks as trace fossils; however, this field includes any and all remains of the activities of living organisms. Thus, a borehole found in a fossil specimen is, per se, a trace fossil, and can be described and discussed in the absence of exact knowledge of the causative agent. Needless to say, there has been some controversy over the "nomenclature" of trace fossils; the International Code of Zoological Nomenclature (ICZN, 1985: Articles 1d, 10d, 42b) currently does recognize "ichnotaxon names," as a parallel nomenclatural system. Häntzschel (1975), Warme & McHuron (1978) and Ekdale et al. (1984) provided excellent reviews of trace fossils.

Predatory boreholes in fossil specimens can be referred to the ichnotaxon "*Praedichnia*" Ekdale, 1985; those produced specifically by mollusks to the ichnotaxon "*Oichnus*" Bromley, 1981; and those identical with naticid boreholes to the ichnotaxon "*Oichnus paraboloides*" Bromley, 1981. Maddocks (1988: 641–2) "arbitrarily defined" 20 "ichnophena" corresponding to different forms of boreholes in ostracod tests; this diversity is unrealistic and meaningless. These names have no heuristic value: if they can be attributed to a known predator, then they should be referred to as "borehole of _____", whereas those of unknown predators should not be given formal names.

ECOLOGICAL ASPECTS OF NATICID PREDATION

This section attempts to integrate and synthesize, from an ecological perspective, the varied aspects of naticid predation. It is hoped that this will not only indicate what has been well documented but also reveal promising (or neglected!) areas for future research. I have not attempted statistically to re-analyze previous studies or to provide detailed criticisms of previous methodologies, unless it seemed directly warranted. Subsequent researchers would be well advised to re-check the relevant previous studies. My section on "Mechanisms of naticid predation" above included the more proximate aspects of naticid prey detection, capture and boring; this section covers the broader, ultimate aspects of naticid predation, as well as several topics from the "prey's viewpoint."

A. Prey Size and Species Choice

The embryos of naticids feed on dissolved organic matter (DOM); some species have yolk reserves or infertile nurse eggs which serve as additional food resources, especially for those with direct development. Naticid species with planktotrophic larvae feed on the phytoplankton while in the swimming stage; those with lecithotrophic larvae undoubtedly rely on DOM in addition to their yolk reserves (Ansell, 1982c).

The feeding habits of juvenile naticids have been much less studied. For example, Ansell (1982c) reported that they ate various unspecified gastropods or bivalves of small size; Berg (1976) was able to feed them *Bittium* and *Rissoella,* although this was limited to aquarium studies. Wiltse (1980a) found that juvenile *Neverita duplicata* at Barnstable Harbor (Massachusetts) consumed the diminutive venerid *Gemma gemma;* because of the high density of the latter, naticid predation accounted for less than 15% of total prey mortality. Maddocks (1988) concluded that juvenile naticids represented significant predators of ostracods; with ontogeny, the naticids shift to larger-sized molluscan prey.

Adegoke & Tevesz (1974: 22) claimed that "no direct correlation was found between prey size and predator size"; but no statistical data were presented to support this statement. Other studies, however, have shown that there is usually a good correlation between predator size (as determined by the inner borehole diameter) and the prey size (e.g. Ansell 1960; Bayliss, 1986; Griffiths, 1981; Kabat & Kohn, 1986; Kitchell et al., 1981; Macé, 1978; Martinell & De Porta, 1982; Robba & Ostinelli, 1975; Selin et al., 1986; Wiltse, 1980a). Colbath (1985) reported little correlation between borehole diameter and prey size, except for *Katherinella* prey. However, these results are a consequence of Colbath's use of bivalve shell "width" rather than the more conventional length as the dimensional measure.

Also of importance is the relative size of the prey taxa and the naticid predators. Large prey species are often less susceptible to predation by naticids than are small prey species. Similarly, within a species, smaller individuals usually suffer greater naticid mortality (e.g. Franz, 1977; Jackson, 1972). Penney & Griffiths (1984) used three-dimensional predation contour diagrams to display the relationships between predator size, prey size, and quantity of prey consumed. Alternatively, Hoffman (1976b: 296) showed no size-selectivity for some (but not all) gastropod prey from the Poland Miocene. However, Green (1968) found that mortality from naticid boring of the bivalve *Notospisula parva* actually increased with prey shell size; similar results were shown by Mukai (1973) and Wilson (1988). As discussed below, increased prey size over geological time may represent an evolutionary response to naticid predation (or is of adaptive value to escape predation) (Kelley, 1984, 1989b).

Prey switching, or prey choice, has been a contentious point; the fundamental question of "why" a given naticid will pick a certain prey species given an equal choice of several species can lead to teleological explanations. Ansell (1983) found that dietary switching will not occur and suggested that "preconditioning" may play a rôle in species choice. Broom (1983) found that younger *Natica maculosa* fed on *Pelecyora trigona,* whereas older predators fed on *Anadara granosa;* ontogenetic dietary switching thus occurred.

Several studies, using a variety of prey items, have determined a hierarchy of preferred prey choices. For *Euspira alderi,* Bayliss (1986: 40) found that the preferred bivalve prey, in descending order, were: *Mya, Spisula, Cerastoderma* and *Parvicardium; Arctica* and *Corbula* were not preyed upon. Similarly, George (1965) found that mortality due to naticids was most prevalent in *Glycymeris glycymeris,* and less so in *Donax semistriatus* and *D. trunculus* (the latter the larger species). Kitchell et al. (1981) found that for *Neverita duplicata,* the preferred prey, in descending order, were: *Mya, Mercenaria, Mytilus* and *Neverita.* Although *Neverita* was actually the highest in energetic value, the handling costs were such that only much smaller conspecific prey could be captured by the naticid predator. Kelley (1989a) found that bivalve prey from the Maryland Miocene were preferentially bored, in descending order, as: *Eucrassatella, Anadara, Astarte* (the latter two roughly equivalent) and *Corbula,* with slight differences from one formation to another.

The same naticid species, in different localities, may have markedly different diets. Thus, *Natica maculosa* in Penang (Malaya) feeds wholly on gastropod prey, especially the trochid *Umbonium vestiarium,* whereas this species at Kuala Selangor (Sumatra) feeds on bivalve prey, particularly *Anadara granosa.* In this case, it is the relative availability of prey taxa which determines (in part) the diet of a given naticid species (Broom, 1982; Berry, 1982).

A recent series of studies by Kitchell and colleagues (Kitchell et al., 1981; DeAngelis et al., 1984, 1985, 1989) have attempted to model the energetic and coevolutionary aspects of naticid ecology. The first study was of value in providing a useful model for the testing of naticid predation; however, the subsequent papers incorporated multiple assumptions which decreased their representation of the real world into a series of parameters couched in advanced equations. This reductionist approach cannot account for complex, stochastic, and hierarchial ecological communities.

It is worthwhile to elaborate briefly the basic principles of the Kitchell models. Essentially, the cost:benefit ratio for various prey species is determined (costs being the time and energy to recognize, capture/subdue, bore, and digest the prey; benefits the energetic value or gain of prey tissues) and related to both prey size and predator size, given that the cost of a specific prey will vary according to the predator size. From this, one can graphically represent the cost-benefit functions with prey size as the dependent variable and cost: benefit ratios as the independent variable. The lowest curve represents the optimal prey choice. These curves show that optimum prey are of intermediate sizes; too-small prey are of low energy value and too-large prey can usually escape the predator. Kitchell (1987) found that these models lead to the prediction that "larger naticid predators should be more highly selective than smaller-sized naticids," all other factors being equal. Discussion of their later models, dealing primarily with predator-prey coevolution has been deferred to section F, under the evolutionary aspects.

Kelley (1982b, 1987, 1989a–b) used these methods to analyze naticid predation in the Maryland Miocene fauna, and confirmed that the models predict prey selection patterns, but with some exceptions. She found that over time, bivalve prey shell thickness (= cost) increased while there was no overall trend in shell volume (= benefit). Commito (1987) questioned the validity of the Kitchell models and noted that their assumptions neglected several important factors with respect to prey defense strategies (or adaptations): ignored were the possibilities of depth refuges, shell ornamentation, chemical defenses, or behavioral responses, all of which could deter naticid predation. DeAngelis et al. (1987) acknowledged these criticisms and suggested that yet further modelling would be able to incorporate these aspects of prey biology. It is difficult to account fully for all the parameters or variables that determine or influence predation processes; any model that attempts to do so would likely be so unwieldy or incomprehensible as to be of little heuristic value.

Interestingly, Ansell (1982b) found that *Euspira alderi* would not feed on opened bivalves—only live, closed prey items were chosen. These same results were found by Kitchell et al. (1986: 297) for *Neverita duplicata.* This suggests that the stereotypy of prey choice restricts the naticids to fresh prey, and rules out scavenging or carrion-feeding.

Predation by naticids on other naticids can be quite widespread and represents a significant source of naticid mortality. Although occasionally referred to as "cannibalism," that term is inappropriate since this predation does not necessarily involve conspecifics. Studies from the Nigerian Eocene showed that about 15% of naticid shells had naticid boreholes (Adegoke & Tevesz, 1974); Colbath (1985) observed only 2.7% such in the Oregon Miocene; Hoffman et al. (1974) noted 10% such in the Poland Miocene. Boekschoten (1967) found that 7.8% of the naticids from the Belgian Pliocene had naticid boreholes. Kabat & Kohn (1986) determined that in the Fijian Pleistocene, naticid predation on *Natica* spp. accounted for 27% of mortality, whereas that on *Polinices* and *Sinum* spp., for only 3% of mortality. The latter genera have more globose shells and a larger foot which may provide faster locomotion and hence facilitate escape from confamilial predators. Maxwell (1988) concluded that smaller-sized naticids of the New Zealand Miocene had much higher naticid predation rates, confirming size-selectivity aspects of naticid predation. Several studies on Recent naticids have also shown extensive confamilial predation (Burch & Burch, 1986; Fretter & Manly, 1979). Obviously, there is considerable variation as to the extent of confamilial naticid predation; disease and predation by fish or crustaceans may represent more important naticid mortality pressures.

B. Stereotypy of Boring on Prey Shell

For gastropod prey, there has been some confusion among studies with respect to the siting of successful boreholes, with some "results" actually of no consequence. Thus, Arua & Hoque (1989a: 55) emphasized that the "preferred drilling site" on the apertural side was on the last whorl; however, because of whorl overlap, most of the exposed prey shell surface **is** the last whorl, and thus purely non-random borehole siting would lead to most boreholes located there (their other results combine 11 prey species into a single table which does not facilitate further analysis). Yet, for some gastropod prey, there is a predominance of predation on the dorsal (abapertural) side over the ventral (apertural) side; this reflects the increased ability of the prey to escape in the latter position (Adegoke & Tevesz, 1974). However, other studies suggested that predation on the ventral side is preferred since the predator's foot seals off the aperture, blocking escape (Berg, 1976: 3; Berry, 1982). Some studies have shown that certain gastropod prey are preferentially bored on the penultimate whorl (rather than the last whorl); this, too, reflects prey handling factors (Dudley & Dudley, 1980; Hoffman & Martinell, 1984). Boreholes that are at either extreme end (apical or abapical) may not allow the proboscis to penetrate the entire shell; more centrally located boreholes may facilitate complete consumption of the prey tissues.

For gastropod prey, it is convenient to analyze the stereotypy of borehole siting by the various geometrical subsets of the shell. Not only can one distinguish between the outer (body) whorl and the older, apical whorls [i.e. the horizontal dimension], but one can also partition the prey gastropod shell whorls into semicircular sectors, or longitudinal zones [i.e. the vertical, or axial dimension]. Thus, Berg (1976) and Berg & Nishenko (1975) developed two conflicting numbering schemes for the latter division. In the 1975 paper (their figure 1b), the sectors (numbered 1–8) started with the apertural plane and proceeded counterclockwise (when viewed from the apex); thus, their clockwise "pie chart" (their figure 1c) of the sectors is actually viewed abapically. But, in the 1976 paper (his figure 2a) the sectors (also numbered 1–8) started with the apertural plane and proceeded clockwise (when viewed from the apex); their clockwise "pie chart" (his figure 2b) is, this time, viewed apically! It is not clear what has been done here; my recommendation is that future investigators explicitly specify which scheme they are using.

Kabat & Kohn (1986: fig. 4), using the first scheme, observed that for naticid prey, boreholes were found in four of the eight shell sectors, with nearly 90% occurring in two 90° sectors; however, there was little overall evidence for stereotypy of borehole siting. Robba & Ostinelli (1975: 327) independently depicted an angular measurement system which corresponds to the first scheme of Berg. Stump (1975: figs. 19–21) devised an elaborate "equal-area projections" system to show frequency-contours (in percentages) of borehole siting on the various prey shells. Regrettably, this method is difficult to visualize and does not lend itself to comparison with the other, more direct schemes; it does not seem to have been used by subsequent authors.

Some studies have shown that most boring occurs near the shell margin of bivalve prey, where the shell is thinner and there is no sculpture (e.g., Ansell, 1960; Ansell & Morton, 1985). Other studies, however, have shown a preference by other naticids for boring near the umbones (e.g. Ansell & Morton, 1985; Arua & Hoque, 1989; Bernard, 1967; Colbath, 1985; George, 1965; Jacobson, 1968; Kitchell et al., 1981; Leidy, 1878; Matsukuma, 1976; Negus, 1975; Piéron, 1933; Thomas, 1976; Vignali & Galleni, 1986); or in the mid-region (Bayliss, 1986; Griffiths, 1981; Vermeij et al., 1989). The strongly inequilateral *Periploma margaritaceum* was primarily bored on the anterior slope, due to its shell form (Rosewater, 1980). Some earlier studies had suggested that naticids preferentially bored near the prey gonads or digestive tissues (Pelseneer, 1924; Verlaine, 1936); however, borehole siting is primarily a function of the manipulation of the prey during boring and may depend on the prey shell morphology. In a few cases, little stereotypy is manifested. Berg & Porter (1974) found that, for the same bivalve prey, there were significant differences between naticid species as to the preferred borehole position; Berg (1975) suggested that behavioral differences in prey capture and handling influenced species-specific patterns.

Probably of greater importance are (1) the size of the prey relative to the predator; (2) the shell thickness and presence or absence of sculptural elements; (3) the relative convexity of the prey shell; (4) other factors relating to the predator's manipulation of the prey. Based on this review, no one element solely determines the locus of borehole siting among bivalve prey.

The majority of studies have shown little preference for right *vs.* left valves of bivalve prey, as would be expected given the equivalve nature of most infaunal bivalves. Some studies have shown 10–20% "differences" in the frequency of boreholes between valves, but no clear trends are apparent. Needless to say, for each valve with a borehole, there is a matching, unbored valve; hence the naticid mortality rate is twice the number of bored valves divided into the total number of valves. It is incomprehensible as to what Lever et al. (1961: 341) meant when they stated that "the percentual mortality may in some cases exceed 100 [%]."

Adegoke & Tevesz (1974) stated that *Varicorbula* from the Nigerian Eocene was pleurothetic and invariably bored on the right valve which is closer to the surface. However, as noted below, the left valve of corbulids has a thick periostracum which deters boring predation; the position of the corbulid shell in the substrate is of less import (De Cauwer, 1985). More generally, since naticids usually manipulate their prey prior to boring, the life position may be of little relevance. Newton (1983) found that the Triassic limid *Mysidioptera* was always bored through the left valve; this taxa is an epibyssate recliner and the left valve is adjacent to the substrate (Newton et al., 1987: fig. 27).

C. Incomplete and Multiple Boreholes; Non-boring Predation

Incomplete boreholes are usually interpreted to represent a sign of interruption of predation, whether by prey escape, arrival of another predator, or other disturbance. In some cases, the same naticid (or another) will recapture the prey and commence boring a new borehole, elsewhere on the prey shell. Sometimes the new hole will coincidentally overlap the older hole; but studies have shown that naticids cannot recognize their own previous borehole and resume drilling there (thereby saving considerable time) (Kitchell et al., 1981: 539). The related problem of multiple complete boreholes again suggests interruption of predation after the completion of a borehole. Obviously there is an evolutionary disadvantage in not recognizing previous boreholes (complete or incomplete); the stereotypy of naticid predatory patterns may not be sufficiently flexible (Vermeij, 1982: 707; Kitchell et al., 1986).

In an analysis of the Miocene *Strioterebrum monidum* from the Caribbean, Kitchell et al. (1986: 294–5) found extremely large numbers of shells with multiple boreholes; one such had 15, of which 12 were incomplete and three had penetrated the prey shell but were not sufficiently wide to allow passage of the proboscis. Further studies on living terebrids by these authors confirmed that some species of this prey family are highly agile and can repeatedly escape naticid predation during the boring actions. Earlier, Vermeij et al. (1980: table 2) showed rather high rates (to 40%) of incomplete boreholes in various Recent terebrids; G. J. Vermeij (*in litt.*) suggested that the pungent odor of terebrids and olivids may represent a chemical defense against predation.

Fischer (1962b: 97) found that in a large sample (n = 1,126) of the Eocene turritellid *Mesalia*, 70.9% had naticid boreholes. Of the bored specimens, 84.8% had a single complete borehole (of which a tenth also had one to several incomplete boreholes); 4.2% had multiple complete boreholes; 8.7% had a single incomplete borehole; and 2.3% had multiple incomplete boreholes. Kitchell et al. (1981: 542) observed that the lucinid *Pseudomiltha floridana* had a ratio of incomplete to complete boreholes of 0.54:1. This taxon was stated to be polymorphic for shell thickness; the thicker shells were more likely to have incomplete boreholes.

An important recent discovery was that some bivalve prey, primarily in the tropics, are preferentially bored through the edge of the valves (Taylor, 1980: 175; Vermeij, 1980: 330); not only is the shell thinner there, but also the prey shell is unsculptured and easier to bore (Ansell & Morton, 1985). The latter authors found that some species (i.e. of *Polinices*) regularly edge-bored *Bassina*, while *Glossaulax* did not; that genus may preferentially bore other prey taxa. Some elements of "learning" (conditioning) may be involved in these responses to shell sculpture.

The razor clams (*Ensis, Solen*) have been shown to be typically consumed by naticids without boring, because when the valves are contracted, there are still sizable pedal and siphonal gapes through which the naticid proboscis can be inserted (Turner, 1955; Edwards, 1975; Schneider, 1981; Frey et al., 1987); this was also shown for *Tresus* (Reid & Fiesen, 1980: 32). Edwards & Huebner (1977) noted that *Mya* was not consumed directly through its large siphonal gape; instead, naticids always bored through the valve; possibly the siphonal tissue deters feeding activities. Earlier, Agersborg (1920: 421) had claimed that *Mya* and various other clams could be suffocated and directly consumed by *Euspira lewisii;* this now seems doubtful. Vermeij & Veil (1978) found that the frequency of gaping bivalves in marine faunas decreased from the Arctic to the tropics and noted that this was correlated with the increase in shell boring and other predation sources in warmer habitats.

Some gastropod prey can be attacked through the aperture, as the corneous operculum is flexible enough for the proboscis to be inserted around the margins (Hughes, 1985). Edwards (1969: 327) found that some *Olivella* prey were consumed without boring, and suggested that either the naticid could force the operculum, or else the prey "suffocates while wrapped in the predator's foot and relaxes," allowing the predator direct access to prey tissues. Interestingly, Yochelson et al. (1983: 11) speculated that the stereotypy of naticid boring precluded their attacking scaphopods directly through the open apertural end; but they suggested that it was more likely that once the scaphopod had retracted posteriorly, the naticid proboscis would not be able to reach the prey tissues.

As mentioned earlier, the tropical Indo-Pacific *Polinices mammilla* is able to "suffocate" and consume bivalve prey without boring. Ansell & Morton (1987) documented that this non-boring predation, in aquarium experiments, accounted for 14% to 54% of the bivalve mortality (according to prey species). This example, and those in the preceding two paragraphs, would greatly complicate community analyses (especially of fossils!) since no "traces" of naticid predation would be left on the post-mortem prey shell.

It should be noted that the results of several studies of naticid predation were misinterpreted as concluding that a significant number of the prey were consumed without boring (Kitchell et al., 1986: 297). Thus, Edwards (1975: 17) found that about 75% of the prey were bored and the remainder died of other causes; Taylor et al. (1980: 397) erroneously took this to mean that the latter 25% of the prey were consumed (by naticids) without being bored. Similarly, Medcof & Thurber (1958) misinterpreted their own data to assume that all the empty, non-bored bivalve prey shells were consumed by naticid predators without boring; this overlooked other mortality sources. Another study (Bernard, 1967) stated that "in limited aquarium observation, over 60% of *Saxidomus* consumed showed no drill marks" (p. 9); and, again, ". . . in aquaria tests 25% of clams [*Saxidomus giganteus*] consumed by *Polinices* [= *Euspira*] *lewisi* bore no marks at all" (p. 10); the discrepancy in numbers is irreconcilable and all bivalve mortality was erroneously attributed to naticid predation.

D. Prey Defense Mechanisms

Ansell (1969) and Carter (1968) provided a general overview of defense mechanisms in various marine mollusks. Many bivalves show leaping or rapid burrowing in response to contact by naticids. Laws & Laws (1972: fig. 1) described the escape response of the Australian *Donacilla angusta,* which leaps or pops out onto the surface, thereby evading the burrowing naticid predator; similar responses were shown for *Ensis directus* (Turner, 1955; Schneider, 1982) and *Ruditapes philippinarum* (Rodrigues, 1986). Either rapid or deep burrowing (or both), can serve as an escape mechanism (Vermeij, 1983a) for bivalve prey.

Ansell & Morton (1985: 656) found that the anomalodesmatan bivalves *Lyonsia* and *Pandora* seemed to escape naticid predation "by coating the posterior edge of the shell with mucus to which sand grains adhere"; presumably this somehow deterred naticid predation.

Corbulid bivalves have been the object of several paleoecological studies; corbulids are noteworthy for their well-developed conchiolin layer (within the valve) which serves as a fairly effective deterrent to gastropod predation (Lewy & Samtleben, 1979). Furthermore, most successful boreholes are in the right valve, since there is well-developed periostracum on the left valve of corbulids which also deters predators. Complete boreholes in corbulid valves have a special form, with a considerably narrowed inner margin below the conchiolin layer (De Cauwer, 1985: figs. 1d, 1e). Kelley (1989a: 446–7) also found considerably reduced successful predation on *Corbula* and suggested that the low level of selectivity of prey size and borehole siting may also account for the high rate of unsuccessful predation (60% of boreholes nonfunctional). Lewy & Samtleben (1979: 350) suggested that the conchiolin layer serves as a compensation for the slow mobility and shallow burrowing of corbulids.

Alternative "defense" strategies of two bivalves were discussed by Commito (1982); *Mya arenaria* grows rapidly to a large size (and deferring reproduction until then), thereby escaping naticid predation [= size refuge], whereas *Macoma balthica* instead grows slowly, reproduces early, and escapes most naticid predation by deep burrowing [= spatial refuge]. Of course, *Mya* is subject to naticid predation while it is still small. The former mechanism was used by Hutchings & Haedrich (1984) to explain the size structure of deep-water nuculanids subject to naticid and fish predation. Actually, these "alternative" life history patterns may represent phylogenetic constraints rather than direct adaptations to naticid predation, per se.

Ansell & Morton (1985) discovered that removal of the sculptural lamellae on the shells of the venerid *Bassina* led to increased boring predation through the shell sides. Otherwise the naticids bored through the valve edges which do not have sculpture. This experimental observation demonstrated the function of sculpture as a prey shell defense mechanism in addition to stabilizing the bivalve in soft sediments.

Bayliss (1986) found that among bivalve prey, the species with the thinnest shell was preferentially preyed upon by naticids. Hingston (1985: table 4) noted that increased prey shell sculpture led to increased frequency of unsuccessful (incomplete) boreholes. Dudley & Vermeij (1978: 439) concluded that strong spiral ribs usually deterred boring in turritellids. Kelley (1982a: 46) reported that uncrenulated (male) shells of *Astarte* were more likely to be bored than were crenulated (female) shells; however this genus is protandrous, and the resulting size differences (between sexes) may be sufficient to explain differences in predation rate (given that the smaller males are less likely to escape predation).

Boggs et al. (1984), using *Mercenaria mercenaria* prey, artificially ground-down the shell surface to half the normal thickness, and tested the effects on predation by *Neverita duplicata.* They found that naticids could not learn to differentiate between normal and thin-shelled prey, although the latter took considerably less time to bore. The same results were found by Rodrigues et al. (1987) for *Neverita didyma* preying on *Ruditapes philippinarum*. In some respects, these studies are of questionable value since it has not been shown that gastropods have any sensory mechanism for "determining" shell thickness (or shell weight). It is true that preying on thinner prey freed up additional time for foraging; surely the snails are incapable of this realization because they have no method for recognizing the thinner prey. This is an interesting case of a hypothetical coevolutionary response that does not initiate an "arms race."

E. Food Webs, Energy Flow and Physiological Efficiencies

Food webs are attempts to diagram the overall trophic structure of an ecological community (predators, herbivores, primary producers, detritivores). Elucidation of the structure of a food web and the strength (or quantity of interactions) of each link (chain) facilitates analyses of community energy flow and population dynamics. As infaunal predators, naticids (with other infaunal polychaetes, crustaceans, and nemerteans) represent an often overlooked level of predation, in addition to the more conspicuous epibenthic predators (asteroids, fish and crabs) (Commito & Ambrose, 1985). An example of the complexity involved is that both asteroids and naticids prey on bivalves, whereas some asteroids also prey on naticids (Christenson, 1970: 67); the same multiple interactions also occur with respect to crabs and fishes. Relatively little research has been done on determining the complete food webs for soft-bottom communities, in contrast to better-known rocky intertidal communities; this reflects the ease of access and analysis of the latter fauna.

Several paleocological studies have attempted to elucidate community structure and food webs, based primarily on an analysis of shell boring and breaking predation (Hoffman & Szubzda, 1976; Stanton & Nelson, 1980; Stanton et al., 1981; Stump, 1975; Taylor et al., 1983). While of great heuristic value in facilitating comparisons between fossil communities (as well as with Recent communities), these studies are limited by the indeterminate nature of mortality that leaves no "traces," as well as shell-removing agents, the latter skewing the results towards the remaining predatory agents.

It is important to realize that naticid predation represents only a part of the sum of all predation in soft-bottom communities; several authors have carefully reviewed the diversity and importance of other predators in these habitats (Cadée, 1968; Carter, 1968; Vermeij, 1978). Thus, Green (1969) found that naticids accounted for 9% of the mortality of the tropical bivalve *Notospisula parva;* shell-crushing skates were responsible for over 60% of the mortality; the remainder was due to other factors (disease or abiotic agents). The latter, non-predatory sources of mortality are just as important but virtually impossible to determine precisely from fossil or beach assemblages (i.e., an empty, undamaged shell may be the outcome of parasitism, other disease, sedimentation, or other agents) (Hoffman, 1976a).

A series of excellent physiological studies was conducted by Ansell and Macé on the European *Euspira alderi*. Distinct periods of shell growth were followed by egg collar production; feeding was considerably greater during the latter stage, since over 90% of non-respired assimilated energy is used for reproduction (Ansell & Macé, 1978; Ansell, 1982a–b). Predation rates increased with temperature (Macé, 1981a); and oxygen consumption rates (= respiration) were affected by the prey type and quantity (Macé, 1981b; Macé & Ansell, 1982). Each week, an adult naticid consumed up to its own (dry) weight in prey tissue [*Tellina tenius*] (Ansell, 1982a); this is limited by the extensive time spent in obtaining suitable prey. Macé (1981c) found that energy assimilation efficiency is about 60% during reproductive periods, and only 40% at other times. About 50–60% of the consumed energy is, however, "lost": not accounted for by growth, respiration (maintenance) or reproduction. Ansell (1982b) suggested that some of this may be accounted for by the mucus that is essential for prey capture and predator avoidance; much of the remainder is represented by feces and unconsumed prey tissue, but Berry (1983) was unable to calculate the energetic costs or losses due to mucus or feces. Bayliss (1986), using the same naticid species, found that about 24% of the time was spent drilling, 11%–18% ingesting prey tissue, and the remaining time in other activities, typically quiescent.

Related physiological studies on the temperate *Neverita duplicata* (in Massachusetts) showed that the feeding season was only about 35 weeks, during which approximately 1.85 prey (*Mya arenaria*) were consumed per week. The naticids consumed about 1% of their body weight in prey on a daily basis, and the overall growth efficiency rates (snail growth in kilojoules per clam tissue consumed in kilojoules) declined from almost 50% in young snails to 16% in older snails (Edwards & Huebner, 1977; Huebner & Edwards, 1981).

Another factor of importance in calculating energy budgets is whether or not all the prey tissue is consumed. Thus, for a high-spired gastropod prey, some of the apical tissues may not be reached by the proboscis. Edwards & Huebner (1977) found that when feeding on *Mya,* only about 80% of the prey tissues were consumed (i.e. the "energy rich, low-ash content tissues"); proboscoidal access is not at issue here and this may reflect the less-palatable nature of the mantle edge and siphonal tissues of *Mya.*

Broom (1982) determined the "consumption rate" equation of feeding efficiency: this represents the mg dry weight of prey consumed per day, as a function of predator body (wet) weight. Thus, for *Natica maculosa* feeding on *Anadara granosa,* the allometric equation was $CW = 9.13\ (W)^{1.0086}$, where $W =$ predator wet weight (in grams). Similarly, Griffiths (1981) found that the consumption rates (of bivalve prey, *Choromytilus meriodionalis*) increased 4.5 fold over a 55% increase in predator (*Natica tecta*) size.

Many of these studies were based on laboratory (aquaria) observations. These, of course, are a simplification or modification of reality (field behavior). Bayliss (1986: 46) cogently noted that "the artificial and enclosed environment in an aquarium increases the predator's ability to detect and capture a prey item as well as reducing the prey's ability to avoid and escape from the predator." Also, intertidal naticids are usually quiescent during low tide; in aquaria where they are continually submerged, the duration of activity is more extensive. Many laboratory studies (e.g. Rodrigues, 1986) used an aquarium sand depth barely greater than the prey or predator size; this does not allow for normal burrowing patterns. Kitchell et al. (1986: 297) noted that in their aquaria, the prey frequently "die, gape and decompose without the predator taking any part in the process"; this suggests that their prey were usually moribund or otherwise unhealthy, and leads one to question the validity of predation studies on these weakened prey. These caveats should be considered when calculating feeding rates, energy budgets, and related trophic measurements based on laboratory studies.

A typical example of the effects of naticid predation on prey population dynamics is that of Ansell (1960) who found that of first-year *Venus* [= *Chamelea*] *striatula,* 40% of the total mortality [= 15% of all individuals] was due to naticids; for the second-year cohort, only 15% of all mortality [= 5% of the cohort] was naticid predation; and for the third-year cohort [the last], only about 1% of all mortality was due to naticids. Clearly, predation by *Euspira alderi* affects primarily the younger cohorts; disease or other predators affect the older cohorts.

Another interesting taphonomic-ecological phenomenon is that of "beach sorting" or the differential post-mortem "survival" of valves of different bivalves (interspecific and intraspecific analyses), comparing both right *vs.* left valves and bored *vs.* unbored valves (Lever et al., 1961; Lever & Thijssen, 1968; Martinell & De Porta, 1980). The critical question is whether or not bored valves are differentially susceptible to post-mortem damage which would affect their representation in the fossil (or "beach shell") assemblage (Dudley & Vermeij, 1978: 437). One must also determine the extent of other shell-breaking predation that wholly removes the shells from the assemblage.

The studies of Lever and colleagues found that valves with boreholes (natural or artificial) traveled shorter distances but were more likely to end up higher on the shore (than non-bored valves), because of the biomechanics of fluid flow through and around bored valves. Thus, the "hole effect" is the upward transport of bored valves. The differential transport of right and left valves may also occur, resulting in greatly distorted ratios thereof in a beach assemblage. Indeed, it is possible that some paleontological studies showing "differences" in boring rates between valves may actually be a consequence of this differential sorting. A problem with such studies is that the hydrodynamic properties of bivalve shells can vary between taxa, and the biomechanical effects of one shell morphology may well be the opposite of those of a different morphology.

F. Enemies and Control of Naticids

Asteroids (starfishes or seastars) are important predators of naticids (Agersborg, 1920; Christenson, 1970); some naticid prey will ward off the asteroid by extension of the foot over the shell followed by mucus secretion (Ansell, 1969; Margolin, 1975). The latter author documented that *Natica stercusmuscarum* could respond to *Astropecten* by rasping off the spines and consuming the tube feet, deterring the starfish. Clarke (1956) noted that *Nassarius trivittatus* feeds upon the egg collars of *Euspira heros,* serving as a means of control. Ironically, this nassariid is, in turn, preyed upon by adult naticids!

Frequently, naticids are "blamed" for observed declines in populations of commercial shellfish (soft shell clams, quahogs, etc.), and oyster beds may be disrupted as naticids burrow through them in search of other prey items (Agersborg, 1920: 420). Because oysters are now more commonly cultivated on stakes or lines off the substrate, this may now be less of a problem. Edwards & Huebner (1977: 1231) cogently noted that "bored shells . . . are thus an exaggerated indicator of [naticid] mortality . . ." because other predators (arthropods, fish, birds, humans) remove or otherwise destroy bivalve shells. These authors further stated that naticid predators are an easy scapegoat to take the blame for ". . . human exploitation patterns, a sensitive issue." The various mechanisms and their success (or lack thereof) for the control of "pests" of shellfish were reviewed by Korringa (1952: 347–351); hand collecting is particularly ineffective (Turner et al., 1948; Medcof & Thurber, 1958). Carriker (1981: 417) suggested that ecological control, involving species-specific pheromones or deterrents, might be successful. There remains the often unacknowledged dilemma that not only is it impractical (or even impossible) to eliminate these predators, but also the resulting impact on the overall community structure and food web may actually be more deleterious than the effects of the predators themselves on the shellfish.

G. Macroevolutionary Patterns and Evolutionary Escalation

If, as claimed by Fürsich & Jablonski (1984), the Triassic boreholes are attributable to naticids, then the parallel evolution of the naticid boring habit twice (Triassic and Cretaceous) undoubtedly reflected the canalization or phylogenetic constraints of shell-boring: there are only so many ways a shell can be bored, and the underlying mechanisms may have remained quiescent in the Naticidae during the Jurassic. However, it remains unclear whether the Triassic predators are indeed naticids, or how the Jurassic naticids may have fed (possibly as scavengers).

Taylor et al. (1980: fig. 16) presented a hypothetical scenario of the evolutionary radiation of gastropod predation. Generalized proboscis probing was subsequently supplemented by pedal manipulation, which led variously to shell boring, wedging, chipping, or pedal suffocation. It can be assumed that these initial stages represented preadaptations to shell boring; however, the specific origins of the complex accessory boring organ remain uncertain. The independent evolution of shell boring in a number of molluscan taxa represents convergent evolution; the structures and processes are not necessarily homologous. (See "Diversity of Boring Predation" above for further comparisons).

The Cretaceous radiation of naticids is part of the Mesozoic marine revolution, involving the increase in diversity of many modern marine predators as a consequence of the "increase in shelled food supply resulting from the occupation of new adaptive zones by infaunal bivalves and by shell-inhabiting hermit crabs" (Vermeij, 1977: 245). Specifically, the shift of bivalves from predominantely epifaunal and byssate forms to infaunal, siphonate forms served as an escape from the then-dominant epifaunal and pelagic predators [cephalopods, asteroids, sharks and marine reptiles] (see also Taylor, 1981: 236) and subsequently led to selection favoring infaunal predators. If the early Mesozoic naticids were not burrowers (as suggested by their shell morphology), then burrowing in combination with shell boring would have opened up a new adaptive zone for the Cretaceous naticids. At the same time, the diversification of other sandy-habitat gastropods (especially turritellids, turrids and terebrids) provided further infaunal prey for naticids (Taylor et al., 1980: 399).

An important biogeographical phenomenon is the pattern of latitudinal diversity (pole–equator) of predatory prosobranch gastropods. For most of these marine families, including the Naticidae, there is a strong increase in species diversity from the poles to the tropical regions (the two exceptions are the Buccinidae and Turridae) (Taylor & Taylor, 1977; Taylor et al., 1980: 381–3). Correlated with this gradient, Dudley & Vermeij (1978: 439) showed a marked equatorward increase in boring predation in *Turritella*. Subsequently Vermeij et al. (1989), for bivalve prey, actually observed an equatorward decrease in the frequency of complete boreholes (and a correlated equatorward increase in the frequency of incomplete boreholes); they suggested that the turritellids were an unexplained exception to this more general pattern.

It appears that since the Cretaceous, the general mechanisms and consequences of naticid predation have not greatly changed. To be sure, the prey sources have changed, not only due to origination and extinction of prey taxa, but also because of changes in prey defense mechanisms. However, the overall "strategy" of naticid predation has persisted for the last 100 million years (Kitchell, 1987). It is possible that the naticids, following their late Cretaceous–early Tertiary adaptive radiation, have now reached their maximum taxonomic diversity (e.g. Sohl, 1969: fig. 1) and are at stasis which may lead to eventual decline in the absence of evolutionary innovations facilitating further expansion. The highly stereotyped nature of naticid predation suggests that their canalization may be so great as to preclude further breakthroughs (but consider the non-boring, suffocation predation of *Polinices mammilla*).

With the rise of muricids in the later Tertiary, the naticids may have shifted from gastropod to bivalve prey, as suggested by Adegoke & Tevesz (1974). Hoffman et al. (1974) noted that in a Miocene assemblage, naticid boreholes were found mostly in smooth prey whereas muricid boreholes were primarily in ribbed (sculptured) prey; however the former prey are more likely to be infaunal than the latter, which may affect these results. Within the Maryland Miocene, Kelley (1982a) found that naticid predation shifted from predominantly bivalve prey in the Calvert and Choptank formations to gastropod prey in the St. Marys Formation, correlated with the increase in diversity of prey gastropods in the latter formation. Kelley's results may be a preservational artifact, as the St. Mary's has a much better representation of gastropods than do the earlier formations (G. J. Vermeij, *in litt.*). Clearly, one also needs to account for changes in the relative abundances of infaunal prey sources; trends as suggested by Adegoke & Tevesz (1974) may not be applicable on a global scale. In addition, the study of naticids has been primarily in a few restricted habitats; more comprehensive analyses of tropical sub-littoral communities may show other naticid predation patterns.

Kelley (1982a) suggested that extensive naticid and other predation on bivalves increased prey species diversity, perhaps by reducing competitive interactions. Although ecologists recognize several factors that affect species diversity, predation is undoubtedly one of the more important, and one that can be easily recognized in the fossil record. Perturbation experiments involving predator-exclusion cages were used by Wiltse (1980b) to analyze the role of the western Atlantic *Neverita duplicata* in its community structure; she found that snail predation and disturbance (due to burrowing) actually decreased the community species diversity by eliminating the rare species and blocking strong competitive interactions.

Kitchell and colleagues (Kitchell et al., 1981; Kitchell, 1982, 1983, 1986; DeAngelis et al., 1984, 1985, 1989) expanded upon their model of the energetics of naticid predation to develop models of coevolution of naticids and their prey. Coevolution, or the reciprocal evolutionary interactions of two taxa, is an important, albeit difficult to quantify, aspect of evolutionary biology. There has been considerable disagreement as to how tightly or broadly coevolution should be defined or restricted. Indeed, almost any evolutionary trend can be "explained" as part of a coevolutionary process (Vermeij, 1982: 711–2). Instead of recognizing coevolution as "all evolution resulting from biological interactions," it is much more useful to restrict it to "reciprocal adaptation involving the heritable traits of two or more species" (Vermeij, 1983b: 311). These models of naticid-prey coevolution are subject to the same caveats mentioned earlier under the discussion of the previous models. Nevertheless, I shall attempt to summarize their scenarios.

First, one can hypothesize that some sorts of evolutionary "arms races" are involved, with the prey evolving various antipredatory adaptations, but with the predator also evolving new or changed features. One consequence is that "multiple adaptive tactics produce multiple directionality" (Kitchell et al., 1981: 550), meaning that diversity may result as different prey follow alternative strategies and the same is true for different predators. This may result in character displacement or other isolating mechanisms resulting in speciation (Kitchell, 1983).

A direct test of these coevolutionary processes, at least for naticid predators, was conducted by Kitchell (1982) who analyzed Marincovich's stratigraphic data for the eastern Pacific Neogene naticid fauna and concluded that predator "efficiency" increased over geological time. Specifically, size, globosity and streamlining of the shell all increased, as did the proportion of apertural area to shell area and the general diversification of morphology (the latter not fully explained). In some respects these are all a consequence of general phyletic size increase, and may not be directly due to coevolution.

Further refinements of their coevolutionary models predicted that in the absence of predators, prey will reproduce early (i.e., at small sizes); whereas in the presence of predators, prey will show delayed reproduction at larger sizes (DeAngelis et al., 1984). More complex age-structured models tested the prey energy-allocation functions (growth vs. reproduction) as a consequence of predation levels, and resulted in three alternative ecological strategies for bivalve prey as coevolutionary responses: delayed reproduction to large size, early reproduction, or increased shell thickness. Needless to say, the numerous assumptions (DeAngelis et al., 1985: 836) severely constrain the value of their coevolutionary model. In particular, they assume that no other factors affect the population dynamics of the naticids or their prey; this overlooks other predators, disease and parasitism, and abiotic mortality sources, all of which (together and severally) are often of greater importance to the prey than are naticids, as has been documented in the other studies discussed herein. Of course, with respect to the evolution of shell morphology, the latter factors are not easily measured or of great significance. The results of their models largely corroborated the conclusions of previous ecological studies.

Edge-boring of bivalve prey represents an escalation in the evolutionary "arms race" as an adaptive response to the presence of prey sculptural elements and shell-thickening. Similarly, non-boring predation (suffocation) also represents an alternative strategy (Ansell & Morton, 1987: 117); the selective advantages presumably entail a reduction in the energetic costs of boring. Further study should reveal whether some prey taxa are resistant to these novel predation mechanisms. The phylogenetic correlations of these two traits remain uncertain; at the present time, they are only known for a few species from the tropical Indo-Pacific.

To briefly summarize these ecological studies: (a) There is a general positive correlation between predator and prey size; size selectivity is shown as larger prey often have a size refuge from predation. (b) Prey defense mechanisms not only help prevent prey capture, but also may lead to interruptions of predation as shown by incomplete boreholes in the prey shell. (c) The successful mode of naticid predation is limited by its seeming stereotypy (inflexibility). (d) The intriguing possibilities of predator-prey coevolution (arms races) remain unproven for specific cases.

FUTURE DIRECTIONS

This review has suggested several areas needing further research. They are tabulated below; readers will undoubtedly recognize yet other problems amenable to future studies.

The detection of prey by naticids remains a puzzle: elucidation of the potential interactions of chemosensory mechanisms (osphradium) vs. echolocation (Kitching & Pearson, 1981). A related mechanistic problem is to determine the precise biochemical constituents of the accessory boring organ secretion in naticids and the mode of function of shell dissolution.

More ecologically oriented approaches could include sophisticated field analyses of prey choice, entailing controlled manipulations and perturbation experiments (remove one species at a time). Further quantification of the various links of soft-bottom community food webs to determine more precisely the quantitative role of naticids in this habitat. Development of methods of ecological control of naticid predators of shellfish.

Paleontologists could analyze Paleocene faunas for gastropod boring predation; and conduct more detailed studies of Jurassic and Early Cretaceous faunas to supply information on changes in predation and shell form during that time (Vermeij, 1987: 238–9). Further study of the phylogenetic position of the Triassic shell borers and the early fossil record of naticids to unravel the complexities of the origin(s) of shell boring of the naticid type.

Study of boring predation from the cold temperature southern oceans and the sub-Antarctic would be most desirable. The presence of several phylogenetically primitive naticid taxa in those faunas would provide further clues as to the relationships between naticid phylogeny and boring predation. It remains uncertain whether the most primitive subfamily, the Ampullospirinae [Triassic?—Recent] are shell borers.

Further research on the geographical and phylogenetic extent of epifaunal predation, non-boring suffocation, and edge-boring would also add to our knowledge of the phylogenetic correlations of predation mechanisms.

CONCLUSIONS

(A) Bored or punched holes in prey shells are made by nine taxa of marine predators: naticid, muricid & capulid snails, octopods, *Pseudostylochus* (Turbellaria) and *Asemichthys* (Pisces), all in mollusk shells; cassid snails in echinoids; *Okadaia* (Nudibranchia) in calcareous polychaete tubes; and nematodes in foraminiferal tests. Some terrestrial zonitid snails are also shell-borers. Shell-crushing predators (sharks, crustaceans) sometimes leave holes in otherwise intact prey shells.

(B) Following prey capture, naticid boring is accomplished by alternate application to the prey shell of the radula and the proboscoideal secretory accessory boring organ. The distinctive naticid borehole is countersunk, with beveled edges.

(C) The data on naticid prey show that many soft-bottom families of bivalves and gastropods are subject to naticid predation. Rocky-habitat taxa escape the infaunal naticids.

(D) Boring predation potentially attributable to naticids originated in the Triassic but shortly became extinct. The naticid boring habit definitively evolved in the Late Cretaceous and has been documented through Holocene faunas, with an unstudied gap in the Paleocene. No clear trends in rates of boring predation since the Cretaceous are obvious.

(E) Most studies have shown a positive correlation between predator size and prey size; also, smaller prey are usually subject to higher rates of naticid predation. Incomplete boreholes reflect interruptions of predation; multiple boreholes demonstrate inflexible stereotypy of naticid boring. Prey defense can take several forms: leaping or burrowing; thick or sculptured shells; chemical defenses; growth to large size; and the corbulid conchiolin layer. Non-boring predation, either through gaping shells or pedal suffocation, greatly confounds ecological studies since no signs of predation are left on the prey shell.

(F) Naticid predation is an important and easily documented link in the food web of marine soft-bottom communities; other predators often crush or remove their prey without leaving recognizable remains.

(G) The evolution of naticid boring predation is part of the Mesozoic marine revolution entailing the diversification of infaunal bivalves and other gastropods which greatly increased naticid prey sources. Evolutionary escalation (defenses) on the part of prey taxa may have occurred since the Cretaceous; attempts to prove specific coevolutionary trends have been unsuccessful.

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APPENDIX

An * indicates that no species was given; "spp." indicates that more than two species of that genus were reported on in one reference. I have not included the taxa reported on by Arua (1989) or Arua & Hoque (1989a–c) due to the questionable nature of their borehole determinations.

A. Class Gastropoda. Subclass Prosobranchia.
Order Archaeogastropoda. Trochoidea. Trochidae:
Calliostoma laugieiri [Vignali & Galleni, 1987]
Gibbula varia [Vignali & Galleni, 1987]
Helicocryptus radiatus [Taylor et al., 1983]
Jujubinus exasperatus [Vignali & Galleni, 1987]
Margarites monolifera [Taylor et al., 1983]
*Monilea** [Kohn, unpub.]
Umbonium vestiarium [Berry, 1982]
Cyclostrematidae:
*Pseudoliotina** [Taylor et al., 1983]
Turbinidae:
*Turbo** [Kohn, unpub.]

Neritoidea. Neritidae:
Nerita funiculata [Hughes, 1985]
N. scabricosta [Hughes, 1985]
Neritina virginea [Jackson, 1972]
Theodoxus luteofasciatus [Stump, 1975]

Order Mesogastropoda. Littorinoidea. Littorinidae:
Littorina littorea [Edwards, 1975]

Rissoidea. Hydrobiidae:
Hydrobia andrussowi [Kojumdjieva, 1974]
Rissoidae:
Alvania alexandrae [Hoffman et al., 1974]
Ihungia ponderi [Maxwell, 1988]
Mohrensternia angulata [Kojumdjieva, 1974]
M. inflata [Kojumdjieva, 1974]
Rissoa inconspicua [Fretter & Manly, 1979]
Rissoina podolica [Hoffman et al., 1974]

Caecidae:
Caecum glabrum [Hoffman et al., 1974]
Vitrinellidae:
*Circulus** [Hoffman et al., 1974]

Cerithioidea. Cerithiidae:
*Argyropeza** [Kohn, unpub.]
*Bittium** [Berg, 1976; Taylor, 1970]
B. reticulatum [Hoffman et al., 1974]
Cerithium europeum [Kojumdjieva, 1974]
C. variabile [Jackson, 1972]
C. vulgatum [Vignali & Galleni, 1987]
*Rhinoclavis** [Kohn, unpub.]
Procerithiidae:
Cirsocerithium gracile [Taylor et al., 1983]
Diastomatidae:
Sandbergeria perpusilla [Hoffman et al., 1974]
Fossariidae:
"Fossarus" granosus [Taylor et al., 1983]
Turritellidae:
Archimediella spirata [Robba & Ostinelli, 1975]
Mesalia spp. [Fischer, 1962]
M. amekiensis [Adegoke & Tevesz, 1974]
M. regularis [Taylor, 1970]
Turritella spp. [Dudley & Vermeij, 1978]
T. badensis [Kojumdjieva, 1974]
T. bieniaszi [Kojumdjieva, 1974]
T. granulata [Taylor et al., 1983]
T. subangulata [Kojumdjieva, 1974]
T. tricarinata [Hoffman & Martinell, 1984]

Stromboidea. Aporrhaidae:
Aporrhais pespelecani [Martinell & Marquina, 1980]
A. uttingerianus [Martinell & Marquina, 1980]
Drepanocheilus calcarata [Taylor et al., 1983]
D. neglecta [Taylor et al., 1983]
Strombidae:
Rimella fissurella [Taylor, 1970]
*Strombus** [Kohn, unpub.]
Tibia unidigitata [Adegoke & Tevesz, 1974]
Hipponicoidea. Hipponicidae:
*Hipponix** [Kohn, unpub.]
Vanikoriidae:
"Vanikoropsis" cf. *albus* [Taylor et al., 1983]

Tonnoidea. Cassidae:
Semicassis wannoensis [Hingston, 1985]
Cymatiidae:
*Cymatium** [Kohn, unpub.]

Suborder Heteroglossa. Cerithiopsioidea. Cerithiopsidae:
Cerithiopsis tubercularis [Hoffman et al., 1974]

Triphoroidea. Triphoridae:
Triphora perversa [Hoffman et al., 1974]

Epitonioidea. Epitoniidae:
Confusiscala fittoni [Taylor et al., 1983]
Epitonium spinosa [Hoffman et al., 1974]

Eulimoidea. Eulimidae:
Eulima subulata [Hoffman et al., 1974]
Strombiformis glaber [Vignali & Galleni, 1987]

Rissoelloidea. Rissoellidae:
*Rissoella** [Berg, 1976]

Order Neogastropoda. Muricoidea. Muricidae:
Blackdownea quadrata [Taylor et al., 1983]
Eupleura caudata [Flower, 1954]
Hadriania craticulata [Martinell & Marquina, 1980]
Hexaplex benedeica [Adegoke & Tevesz, 1974]
*Morula** [Kohn, unpub.]
Nassa restitutiana [Kojumdjieva, 1974]
N. dujardini [Hoffman et al., 1974]
Paramorea lineata [Taylor et al., 1983]
*Pterynotus** [Adegoke & Tevesz, 1974]
Terefundus lamelliferus [Maxwell, 1988]
Urosalpinx [Flower, 1954]
Buccinidae:
*Cantharus** [Kohn, unpub.]
*Phos** [Kohn, unpub.]
*Siphonalia** [Kohn, unpub.]
Columbellidae:
*Mitrella** [Adegoke & Tevesz, 1974]
M. minor [Hoffman & Martinell, 1984]
M. nassoides [Kojumdjieva, 1974]
Nassariidae:
Amyclina spp. [Robba & Ostinelli, 1975]
*Cyllene** [Adegoke & Tevesz, 1974]
Dorsanum duplicatum [Kojumdjieva, 1974]
Nassarius elatus [Hoffman & Martinell, 1984]
N. italicus [Martinell & Marquina, 1980]
N. obsoletus [Edwards, 1975]
N. perpinguis [Berg & Nishenko, 1975]
N. pygmaeus [Hoffman & Martinell, 1984]
N. semistriatus [Hoffman & Martinell, 1984]
N. tiarula [Stump, 1795]
N. trivittatus [Edwards, 1975]
Niotha crassigranosa [Hingston, 1985]
Plicarcularia leptospira [Broom, 1983]
Fasciolariidae:
*Colubraria** [Kohn, unpub.]
Falsicolus tangituensis [Maxwell, 1988]
*Fusinus** [Kohn, unpub.]
*Granulifusus** [Kohn, unpub.]
Iscafusus rigidus [Taylor et al., 1983]
Latirus moorei [Stanton et al., 1981]
*Peristernia** [Kohn, unpub.]
Turbinellidae [= Vasidae]:
Exilla wellmani [Maxwell, 1988]
Olividae:
Alocospira papillata [Hingston, 1985]
Ancilla buccinoides [Taylor, 1970]
Olivella biplicata [Edwards, 1969]
Marginellidae:
Marginella spp. [Taylor, 1970]
Protoginella bembix [Maxwell, 1988]
Mitridae:
*Cancilla** [Kohn, unpub.]
Mitra orientalis [Kojumdjieva, 1974]
*Scabricola** [Kohn, unpub.]
*Subcancilla** [Kohn, unpub.]
Volutomitridae:
Microvoluta nodulata [Maxwell, 1988]

Costellariidae [= Vexillidae]:
_Austromitra_* [Hingston, 1985]
_Vexillium_* [Kohn, unpub.]

Cancellarioidea. Cancellariidae:
Bonellitia amekiensis [Adegoke & Tevesz, 1974]
B. serrata [Martinell & Marquina, 1980]
Inglisella parva [Maxwell, 1988]
I. allophyla [Maxwell, 1988]
Sydaphera wannonensis [Hingston, 1985]

Conoidea. Conidae:
Conus dujardini [Kojumdjieva, 1974]
C. parisiensis [Taylor, 1970]
Turridae:
Bela brachystoma [Hoffman & Martinell, 1984]
B. vulpecula [Hoffman & Martinell, 1984]
Brachytoma obtusangula [Martinell & Marquina, 1980]
_Clavatula_* [Adegoke & Tevesz, 1974]
Clavus spp. [Robba & Ostinelli, 1975]
Comitas nana [Maxwell, 1988]
_Crassispira_* [Kohn, unpub.]
Cythara subcylindrata [Hoffman et al., 1974]
Eopleurotoma spp. [Adegoke & Tevesz, 1974]
_Gemmula_* [Kohn, unpub.]
Genota ramosa [Kojumdjieva, 1974]
Hesperiturris nodocarinatus [Stanton et al., 1981]
Heterocithara marwicki [Maxwell, 1988]
_Lophitoma_* [Kohn, unpub.]
Mauidrillia occidentalis [Maxwell, 1988]
Michela trabeatoides [Stanton et al., 1981]
Mioawateria personata [Maxwell, 1988]
Paracomitas beui [Maxwell, 1988]
_Pleurotoma_* [Adegoke & Tevesz, 1974]
Raphitoma hispidula [Hoffman et al., 1974]
_Rugobela_* [Maxwell, 1988]
Splendrillia vellai [Maxwell, 1988]
_Tomopleura_* [Maxwell, 1988]
Turricula africana [Adegoke & Tevesz, 1974]
T. dimidiata [Martinell & Marquina, 1980]
Viridoturris powelli [Maxwell, 1988]
Terebridae:
Gemmaterebra catenifera [Hingston, 1985]
Strioterebrum monidum [Kitchell et al., 1986]
S. pliocenicum [Martinell & Marquina, 1980]
Terebra spp. [Vermeij et al., 1980]
T. dislocata [Kitchell et al., 1986]
Zeacuminia viapollentia [Maxwell, 1988]

Subclass Heterobranchia. Superorder Allogastropoda.
Architectonicoidea. Architectonicidae:
Architectonica bendeica [Adegoke & Tevesz, 1974]
A. olicatum [Taylor, 1970]
Philippia meditteranea [Vignali & Galleni, 1987]
Pyramidelloidea. Pyramidellidae:
Eulimella conulus [Hoffman et al., 1974]
Evelynella doliella [Maxwell, 1988]
_Odostomia_* [Adegoke & Tevesz, 1974]
O. conoidea [Hoffman & Martinell, 1984]
Pyramidella digitalis [Hoffman et al., 1974]
P. plicosa [Hoffman & Martinell, 1984]
Pyrgulina interstincta [Hoffman et al., 1974]
Tubonilla rufa [Hoffman & Martinell, 1984]
T. zesulcata [Maxwell, 1988]
Waikura elevata [Maxwell, 1988]

Subclass Opisthobranchia. Order Cephalaspidea.
Philinoidea. Acteonidae:
Acteon reussi [Hoffman et al., 1974]
A. semistriatus [Hoffman & Martinell, 1984]
A. tornatilis [Vignali & Galleni, 1987]
Tornatellaea affinis [Taylor et al., 1983]
T. unisulcata [Taylor et al., 1983]
Ringiculidae:
Avellana incrassata [Taylor, et al., 1983]
Ringicula auriculata [Hoffman et al., 1974]
R. buccinea [Hoffman & Martinell, 1984]
Scaphandridae:
Acteocina lajonkaireana [Kojumdjieva, 1974]
Cylichna melitopolitana [Kojumdjieva, 1974]
C. rubignosum [Kojumdjieva, 1974]
_Scaphander_* [Adegoke & Tevesz, 1974]
Tornatina heraclitica [Hoffman et al., 1974]
T. trunculata [Hoffman et al., 1974]
Hamineidae:
Atys miliaris [Hoffman et al., 1974]
Retusidae:
Retusa kelloggi [Stanton et al., 1981]
R. truncatula [Hoffman & Martinell, 1984].

B. Class Bivalvia. Subclass Protobranchia. Order Nuculoida.
Nuculoidea. Nuculidae:
Acila conradi [Colbath, 1985]
Ennucula kalimnae [Hingston, 1985]
Nucula antiquata [Taylor et al., 1983]
N. mixta [Taylor, 1970]
N. nucleus [Hoffman & Szubzda, 1976]
N. obtusa [Taylor et al., 1983]
N. turgida [Wilson, 1988]
Palaeonucula strigilata [Fürsich & Jablonski, 1984]

Nuculanoidea. Nuculanidae:
Mesosaccella angulata [Taylor et al., 1983]
M. lineata [Taylor et al., 1983]
_Nuculana_* [Adegoke & Tevesz, 1974]
Nuculana spp. [Colbath, 1985]
N. fragilis [Kojumdjieva, 1974]
N. pella [Vignali & Galleni, 1987]
N. pernula [Hutchings & Haedrich, 1984]
Yoldiidae:
_Yoldia_* [Colbath, 1985]
Y. thraciaeformis [Hutchings & Haedrich, 1984]
Malletiidae:
_Malletia_* [Kohn, unpub.]

Subclass Pteriomorphia. Order Mytlioida.
Mytiloidea. Mytilidae:
Choromytilus meriodionalis [Griffiths, 1981]
Crenella orbicularis [Taylor et al., 1983]
Modiolus auriculatus [Vermeij, 1980]
M. reversa [Taylor et al., 1983]
Mytilus edulis [Edwards, 1975]

Order Arcoida. Arcoidea. Arcidae:
Anadara spp. [Kelley, 1989a]
A. elevata [Dudley & Dudley, 1980]
A. granosa [Broom, 1982]
A devincta [Colbath, 1985]
A. diluvii [Kojumdjieva, 1974]
A. thisphila [Dudley & Dudley, 1980]
Barbatia irregularis [Taylor, 1970]
*Bathyarca** [Maxwell, 1988]
Noetiidae:
Arcopsis dissimilis [Darragh & Kendrick, 1980]
Pachecoa declivis [Kitchell, 1982]
Cucullaeidae:
Idonearca glabra [Taylor et al., 1983]

Limopsoidea. Limopsidae:
Limopsis chapmani [Darragh & Kendrick, 1980]
L. beaumarisensis [Hingston, 1985]
L. minuta [Kojumdjieva, 1974].
Glycymerididae:
Glycymeris spp. [Thomas, 1976]
G. albolineata [Matsukuma, 1977]
G. halli [Hingston, 1985]
G. insubrica [Vignali & Galleni, 1987]
G. pulvinata [Taylor, 1970]
G. vestita [Matsukuma, 1977]
Glycymerita sublaevis [Taylor et al., 1983]
G. umbonata [Taylor et al., 1983]

Pterioida. Pterioidea. Cassianellidae:
Cassianella ampezzana [Fürsich & Jablonski, 1984]

Order Limoida. Limoidea. Limidae:
Mysidioptera williamsi [Newton, 1983]

Order Ostreoida. Ostreoidea. Gryphaeidae:
Amphidonte obliquata [Taylor et al., 1983].

Pectinoidea. Pectinidae:
Chlamys radians [Guerrero & Reyment, 1988]
Pectin opercularis [Boekschoten, 1967]
Pseudamussium similis [Smith, 1932].

Subclass Paleoheterodonta. Order Trigonioida.
Trigonioidea. Trigoniidae:
Rutitrigonia eccentrica [Taylor et al., 1983]

Subclass Heterodonta. Order Veneroida.
Lucinoidea. Lucinidae:
Codakia bella [Vermeij, 1980]
C. orbicularis [Jackson, 1972]
Ctena decussata [Vignali & Galleni, 1987]
C. orbiculata [Jackson, 1972]
Divaricella ornata [Kojumdjieva, 1974]
D. divaricata [Vignali & Galleni, 1987]
*Epicodakia** [Kohn, unpub.]
Loripes dentatus [Hoffman et al., 1974]
L. lacteus [Vignali & Galleni, 1987]
Lucina anodonta [Kelley, 1989a]
L. approximata [Stump, 1975]
L. spinifera [Kojumdjieva, 1974]
Lucinella divaricata [Hoffman & Martinell, 1984]
Myrtea papatikiensis [Maxwell, 1988]
Parvilucina costata [Jackson, 1972]
Pseudomiltha floridana [Kitchell et al., 1981]
*Wallucina** [Vermeij, 1980]
Fimbriidae:
Mutiella canaliculata [Taylor et al., 1983]
Ungulinidae:
Diplodonta subquadrata [Vermeij et al., 1989]

Carditoidea. Carditidae:
Beguina diversicosta [Kojumdjieva, 1974]
Cardita spp. [Adegoke & Tevesz, 1974]
C. chamaeformis [Boekschoeten, 1967]
Cyclocardia subtenta [Colbath, 1985]
Venericardia greggiana [Kitchell, 1982]
V. serrulata [Taylor, 1970]
*Vetericardiella** [Kitchell, 1986]

Crassatelloidea. Astartidae:
Astarte spp. [Boekschoten, 1967; Kelley, 1989a]
Astarte triangularis [Smith, 1932]
Eriphyla striata [Taylor et al., 1983]
Lirodiscus tellinoides [Siler, 1965]
Nicaniella formosa [Taylor et al., 1983]
Crassatellidae:
Crassatella spp. [Taylor, 1970]
C. vadosa [Sohl, 1969]
*Crassatellites** [Kohn, unpub.]
Eucrassatella spp. [Kelley, 1982a]

Cardioidea. Cardiidae:
Acanthocardia tuberculata [Vignali & Galleni, 1986]
Cardium spp. [Smith, 1932]
C. politionanei [Kojumdjieva, 1974]
Cerastoderma edule [Bayliss, 1986]
Clinocardium nuttallii [Bernard, 1967]
Dinocardium robustum [Kornicker et al., 1963]
Fragum fragum [Vermeij, 1980]
Laevicardium elenense [Vermeij et al., 1989]
Loxocardium bouei [Taylor, 1970]
Parvicardium scabrum [Bayliss, 1986]
Protocardia hillana [Taylor et al., 1983]
Thetis laevigata [Taylor et al., 1983]

Mactroidea. Mactridae:
Mactra angulata [Taylor et al., 1983]
M. australis [Laws & Laws, 1972]
M. chinensis [Vermeij et al., 1989]
M. fragilis [Paine, 1963]
M. stultorum [Vignali & Galleni, 1987]
Mactrellona exoleta [Vermeij et al., 1989]
Notospisula parva [Green, 1968]
Pseudocardium sachalinense [Vermeij et al., 1989]
Spisula elliptica [Bayliss, 1986]
S. solidissima [Franz, 1977]
S. subtruncata [Bayliss, 1986]
Tresus nuttallii [Reid & Friesen, 1980]
Mesodesmatidae:
Atactodea striata [Ansell & Morton, 1987]
Coecella chinensis [Ansell & Morton, 1987]
Donacilla angusta [Laws & Laws, 1972]
Ervilia ousilla [Hoffman & Szubzda, 1976]
E. dissita [Kojumdjieva, 1974]

Solenoidea. Solenidae:
Ensis directus [Schneider, 1982]
Solen conradi [Colbath, 1985]
S. strictus [Frey et al., 1987].

Tellinoidea. Donacidae:
Donax spp. [Vermeij et al., 1989]
D. faba [Ansell & Morton, 1987]
D. semistriata [Vignali & Galleni, 1987]
D. trunculus [Vignali & Galleni, 1987]
D. vittatus [Negus, 1975]
Plebidonax deltoides [Kitching & Pearson, 1981]
Psammobiidae:
Gari hamiltonensis [Hingston, 1985]
Tagelus peruvianus [Vermeij et al., 1989]
Scrobiculariidae:
Scrobicularia plana [Richter, 1962]
Solecurtidae:
Solecurtus antiquatus [Kojumdjieva, 1974]
Tellinidae:
Arcopagia robusta [Vermeij, 1980]
Macoma albaria [Colbath, 1985]
M. arctata [Colbath, 1985]
M. balthica [Commito, 1982]
M. calcarea [Aiken & Risk, 1988]
M. nasuta [Reid & Gustafson, 1989]
Palaeomoera inaequalis [Taylor et al., 1983]
Peronidia venulosa [Vermeij et al., 1989]
Quidnipagus palatam [Vermeij, 1980]
*Scissulina** [Vermeij, 1980]
Tellina spp. [Vermeij et al., 1989]
T. donacina [Vignali & Galleni, 1987]
T. emacerata [Colbath, 1985]
T. lux [Broom, 1983]
T. planata [Kojumdjieva, 1974]
T. pudica [Broom, 1983]
T. pulchella [Vignali & Galleni, 1987]
T. tenuis [Ansell, 1982a–c]
Tellinella virgata [Nakamine & Habe, 1983]
Temnoconcha cognata [Vermeij et al., 1989]

Arcticoidea. Arcticidae:
Arctica islandica [Christensen, 1970]
Epicyprina angulata [Taylor et al., 1983]
E. subtruncata [Taylor et al., 1983]
Venilicardia lineolata [Taylor, et al., 1983]

Veneroidea. Veneridae:
Anomalocardia squamosa [Ansell & Morton, 1987]
A. squamosa [Taylor, 1980]
Aphrodina nitidula [Taylor, 1970]
Bassina calophylla [Ansell & Morton, 1985]
Callistina plana [Taylor et al., 1983]
Calpitaria distincta [Taylor, 1970]
Calva subrotunda [Taylor et al., 1983]
Chamelea gallina [Guerrero & Reyment, 1988a]
Chimela caperata [Taylor et al., 1983]
Chione spp. [Smith, 1932]
C. basteroti [Kojumdjieva, 1974]
C. californensis [Stump, 1975]
C. cancellata [Paine, 1963]
C. subrugosa [Vermeij et al., 1989]
C. undatella [Peterson, 1982]
Circomphalus subplicatus [Hoffman & Szubzda, 1976]
Costacallista laevigata [Taylor, 1970]
Dosinia dunkeri [Vermeij et al., 1989]
D. lupinus [Vignali & Galleni, 1987]
Flaventia ovalis [Taylor et al., 1983]
Gafrarium minimum [Smith, 1932]
G. pectinatum [Vermeij, 1980]
Gemma gemma [Wiltse, 1980a]
Gouldia minima [Vignali & Galleni, 1987]
Katelysia scalarina [Laws & Laws, 1972]
Katherinella angustifrons [Colbath, 1985]
Macrocallista nimbosa [Paine, 1963]
Megapitaria squalida [Vermeij et al., 1989]
Mercenaria mercenaria [Berg & Porter, 1974]
M. campechiensis [Paine, 1963]
Meretrix lusoria [Vermeij et al., 1989]
Paraesa faba [Taylor et al., 1983]
Pelecyora trigona [Broom, 1983]
Periglypta reticulate [Vermeij, 1980]
Pitar spp. [Vermeij et al., 1989]
P. morrhuana [Jacobson, 1965]
Placamen subroboratum [Hingston, 1985]
Protothaca spp. [Vermeij et al., 1989]
P. staminea [Peterson, 1982]
Ruditapes philippinarum [Rodrigues, 1986]
Saxidomus giganteus [Bernard, 1967]
Sunetta gibberula [Hingston, 1985]
Tapes japonica [Hamada, 1961]
T. philippinarum [Ansell & Morton, 1987]
Timoclea marica [Vermeij, 1980]
Tivela spp. [Vermeij et al., 1989]
Venerupis aurea [Vignali & Galleni, 1987]
V. senegalensis [Vignali & Galleni, 1987]
Venus multilamella [Kojumdjieva, 1974]
V. striatula [Ansell, 1960]
V. verrucosa [Vignali & Galleni, 1987]
Veremolpa micra [Mukai, 1973]
Glauconomidae:
Glauconome chinensis [Ansell & Morton, 1987]

Order Myoida. Myoidea. Myidae:
Cryptomya californica [Watkins, 1974]
Mya arenaria [Edwards, 1975]
Corbulidae:
*Caestocorbula** [Kitchell, 1986]
Caryocorbula deusseni [Kitchell, 1982]
Corbula spp. [De Cauwer, 1985]
Corbula carinata [Kojumdjieva, 1974]
C. elegans [Taylor et al., 1983]
C. gibba [Vignali & Galleni, 1987]
C. idonea [Kelley, 1989a]
C. rugosa [Taylor, 1970]
C. truncata [Taylor et al., 1983]
Notocorbula ephamilla [Hingston, 1985]
N. innerans [Maxwell, 1988]
Varicorbula amekiensis [Adegoke & Tevesz, 1974]
Vokesula aldrichi [Kitchell, 1982]

Hiatelloidea. Hiatellidae:
Hiatella arctica [Aitken & Risk, 1988]
Panopea mandibula [Taylor et al., 1983]

Subclass Anomalodesmata. Pandoroidea. Periplomatidae:
Cochlodesma leanum [Rosewater, 1980]
Periploma spp. [Rosewater, 1980]

Poromyoidea. Cuspidariidae:
Cuspidaria cuspidata [Hoffman & Martinell, 1984]

C. Scaphopoda.

Dentaliidae:
Dentalium complexum [Fankboner, 1969]
D. bedensis [Kojumdjieva, 1974]
D. spp. [Yochelson et al., 1983]
Fustiaria miocaenica [Hoffman et al., 1974]
Entalinidae:
Entaliopis brevis [Yochelson et al., 1983]
Gadilidae:
*Cadulus** [Yochelson et al., 1983]

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PREDATORY ECOLOGY OF NATICID GASTROPODS WITH A REVIEW OF SHELL BORING PREDATION

Alan R. Kabat

Museum of Comparative Zoology, Harvard University,
Cambridge, Massachusetts 02138 U.S.A.

ABSTRACT

This review provides a critical synthesis and analysis of the extensive body of knowledge of prédation by the Naticidae, a cosmopolitan family of burrowing marine gastropods. First, the diversity of shell boring prédation is reviewed and documented for ten taxa (nine marine, one terrestrial), in order to facilitate comparative analyses. These predators are: Naticidae, Muricidae, Cassidae and Capulidae (Gastropoda, Prosobranchia); Okadaia (Gastropoda, Opisthobranchia): Aegopinella (Gastropoda, Pulmonata): Octopus (Cephalopoda): Pseudostylochus (Turbellaha); Nematoda: and Asemichthys (Pisces). Second, the proximate mechanisms of naticid prédation are explicated. Third, the known prey of naticids are tabulated: over 80 families of gastropods and bivalves are subject to naticid prédation which is essentially restricted to soft-substrate prey taxa. Fourth, the fossil record of naticid prédation is summarized: this prédation dates from the Cretaceous, with a possible boring "experiment" in the early Triassic. The diagnostic countersunk naticid boreholes are recognizable in fossil and Recent faunas: naticid prédation is a readily documented aspect of the otherwise elusive soft-bottom food web. Fifth, the studies on physiology and ecology of naticid prédation are integrated into a conceptual framework. These aspects of naticid prédation (energy budgets, prey size and species choice, unsuccessful prédation) indicate a successful albeit rather stereotyped mode of prédation. The macroevolutionary implications (escalation, or "arms races ') suggest generalized predator-prey coevolution.

Key words: Naticidae, prédation, boring.

DIVERSITY OF BORING PREDATION

In the Mollusca, many of the post-Paleozoic Gastropoda are predators, and an extensive body of research has developed around various aspects of prédation by mollusks (Kohn, 1 983). Most of these studies treat Recent mollusks, including the community ecology, behavior and physiology of prédation. Other, more restricted, studies on fossils analyzed those elements of prédation revealed by fossil shells (boreholes and other signs of shell damage and repair) (Kohn, 1985). Among the predatory gastropods, several families include shell borers which excavate a hole in the prey shell to provide access to the prey flesh. Earlier overviews of boring by gastropods by Fischer (1922, 1966), Carhker (1961), Fatten & Roger (1968), Sohl (1969), Bishop (1975), Boucot (1981: 200 ff.), Bromley (1981), Benton (1986) and Vermeij (1987) have summarized some of this research. More general reviews of gastropod feeding biology were provided by Ankel (1938), Fretter & Graham (1962: 240-262), Taylor et al. (1980), Kohn (1983) and Tsikhon-Lukanina (1987). Inevitably, numerous previous studies have been overlooked by subsequent researchers; this paper seeks to provide some unity and a coherent framework to the body of knowledge of shell boring prédation by gastropods of the family Naticidae.

The objectives of this paper are: (1) to document the diversity of shell boring prédation and related phenomena; (2) to summarize the mechanical or proximate aspects of naticid prey capture and boring; (3) to tabulate the known naticid prey taxa in order to indicate the prey diversity in relation to the overall diversity of marine mollusks; (4) to review the fossil record of naticid prédation in the Mesozoic and Cenozoic; and (5) to integrate and synthesize the ecological and evolutionary aspects of naticid prédation into a broader conceptual framework.

The diversity of molluscan shell boring

predators is briefly reviewed, in order to be able to distinguish amongst the traces of prédation left by the various taxonomic groups of predators. Based on this review, it is obvious that prédation by boring in taxa other than the Naticidae and Muricidae is seldom studied.

Shell breaking predators, particularly crustaceans and fish, represent an entire field of study in themselves; valuable reviews are provided by Vermeij (1978, 1983c). Not mentioned herein are the diverse groups of symbiotic (non-predatory) epibionts and endolithic shell burrowers, such as certain cyanobacteria, fungi, algae, sponges, polychaetes, sipunculans, barnacles, lithophagid and pholadid bivalves, brachiopods and bryozoans (reviewed by Boekschoten, 1966, and the 1969 American Zoologist [vol. 9. #3] symposium on calcibiocavitology). Generally speaking, the latter "bore holes" can be recognized by their large number on a single shell, the lack of complete penetration, and their obvious burrowing aspect. An exception is the pedicle attachment scar of brachiopods, which may show complete penetration in the host shell (often another brachiopod); these scars or holes (common in the Paleozoic) could be confused with those of other, unknown. Paleozoic borers.

Within the Prosobranchia, there are two major groups of shell boring (or drilling) predators, the Naticidae (Mesogastropoda) and the Muricidae (Neogastropoda). I have summarized only a small part of the extensive research on muricid prédation, and have limited it to the principal means of distinguishing their prédation from naticid prédation. A comprehensive review of muricid prédation will be most useful but remains to be wntten.

An heuristic definition of gastropod boreholes was provided by Carriker & Yochelson (1968: 2) as "an excavation of charactehstic size and form dnlled by a predatory snail in the calcareous exoskeleton of a prey organism by means of chemical weakening and radular abrasion of the prey shell for the purposes of obtaining food." Refinements of this definition were provided by Chatterton & Whitehead (1987: 68). Specifically, naticid boreholes are parabolic holes (straight or oblique), formally referred to as a "truncated spherical paraboloid"; the borehole is countersunk (i.e., the enlarged outer margin is beveled or tapered, forming a chamfer) (Fig. 1), and incomplete naticid boreholes are charactenzed by a prominent central boss (rounded elevation) on the bottom surface (Fig. 2).

The Muricoidea (Neogastropoda) is a diverse group containing a variety of eclectic predators, including shell borers, carnon feeders, and other specialized predators, as well as several herbivores. The majority of

muricids are shell borers and are distinguished by the presence of the accessory boring organ (ABO) in the sole of the foot. The muricid borehole is cylindrical, with nearly straight edges (Fig. 3); the naticid borehole, in contrast, has a more parabolic form and beveled edges. Much of the research carried out on the oyster drill, Urosalpinx cinerea, and other shellish pests by Carriker, along with research on other muricoideans by Taylor, has greatly added to our knowledge of the feeding biology of this superfamily (Carriker, 1981; Taylor et al., 1980).

The Nassariidae, or mudsnails, are carnivorous or scavenging members of the Neogastropoda. Fischer (1962a: 75) and Reyment (1966: 34) stated in passing that nassahids are shell borers. Subsequently, Nina (1987; 23) also mentioned that they probably are shell borers. This appears to be mistaken, as no documentation has ever been provided for boring by mudsnails. Similarly, Stevanovic (1950) thought that the boreholes in mollusks from the Serbian Upper Miocene were caused by the hydrobiid gastropod Sandria [= Pseudamnicola] atava: Nina (1987; 25) rejected this conclusion and attributed the boreholes to the naticid Euspira helicina.

The Cassidae (Tonnoidea, Mesogastropoda) are important predators of tropical echinoids, using sulfuric acid from their proboscis gland along with the radula to penetrate the echinoid test (by cutting out a disc, rather than dniling a hole) (Fig. 4). Hughes &

Hughes (1981) provided a comprehensive review of the biology and ecology of cassid prédation, and pointed out that other tonnoideans which feed on mollusks do so without boring (i.e., by penetrating between the gastropod operculum and shell, or between the valves of a clam). The numerous unique aspects of cassid prédation clearly suggest an independent origin from that of naticids or muricids. Tertiary echinoids with cassid holes were documented by Sohl (1969: figs. 7-8) and Beu et al. (1972).

The Capulidae (Mesogastropoda) are specialized ectoparasitic symbionts of mollusks and echinoderms. They are known to drill holes into the shell of their mollusk host for the purpose of obtaining small amounts of fluids from the host's feeding current for nutrition. Matsukuma (1978) reviewed shell boring by capulids and recorded several fossil records of capulid boreholes: these are sharp-sided cylindrical holes, similar to those produced by muricids. However, capulid

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boreholes can be recognized by the surrounding attachment scar on the host shell, where the edge of the capulid shell had slightly worn away the host shell (Figs. 5, 6).

In the Opisthobranchia, the nudibranch Okadaia elegans (Vayssiereidae) is known to drill holes into the calcareous tubes of serpulid and spirorbid polychaete annelids (Young, 1 969). These minute bore holes (Figs. 7, 8) are similar in shape to those of muricids; however, muricids are not known to prey on these polychaetes, whereas Okadaia does not feed on mollusks.

In the Pulmonata, the terrestrial Aegopinella (Zonitidae) are known as shell-boring predators of other gastropods. Mordan (1977: 65) described prédation by A. nitidula. in which prey snails (typically other zonitids) are first attacked through the aperture (followed by consumption of the head-foot); subsequently, a quite irregular hole on the umbilical surface of the last whorl is bored (Fig. 1 1), allowing the predator access to the rest of the prey flesh. Pulmonate shell boring may have evolved from simple shell "radulation," or the scraping of the outer surface of prey shells (Mordan, 1977: 70-1).

In the Cephalopoda, the octopuses are shell boring predators of a variety of marine shelled mollusks (Ambrose, 1986; Nixon & Maconnachie, 1988). Octopus boreholes can be recognized by their distinctly irregular or oval (but not circular) outline and their extremely small inner borehole diameter, in contrast to the large outer borehole diameter (Ambrose et al., 1988) (Fig. 9). Furthermore, the purpose of the hole is solely for the injection of venom to relax or kill the prey, which is then extracted through the aperture or valve opening. One problem with the analysis of octopus prédation is that octopuses frequently break open the shell or otherwise capture the prey without drilling the shell (Ambrose, 1986: table 1). Hence, octopus boreholes represent only part of their trophic activities. Probable octopus boreholes from the Pliocene were reported by Robba & Ostinelli (1975: 338-344).

An unusual polyclad turbellarian flatworm, Pseudstylochus ostreophagus, is known to bore a hole in the shell of juvenile oysters (spat), effecting separation (or relaxation) of the prey adductor muscle, which causes the shell valves to gape, facilitating entry of the predator between the valves leading to prey consumption. The irregular oval holes are quite small (typically 150 x 190 fxm); further details are provided by Woeike (1957). Many

polyclads are known predators of mollusks, but shell boring has not been shown for other species (Galleni et al., 1980: table 1).

Nematode worms are known to prey upon the microscopic Foraminifera (Granuloreticulosa), boring one or more holes in the test, entering the chamber, and slowly consuming the prey. In the past, such holes were thought to be produced by juvenile gastropods (Livan, 1937: 149; Saidova & Beklemishev, 1953; but see Fischer, 1962a: 70-1); however, their size (less than 60 fxm in diameter) is smaller than those produced by newly hatched predatory gastropods (boreholes 100-160 . in diameter). Sliter (1 971) found that nematodes were responsible for this prédation, and illustrated the various borehole morphologies (irregular oval to bevelled round). Subsequently, Arnold et al. (1985) deschbed even larger boreholes (10-125 \\ in diameter) in Foraminifera from the Galápagos hydrothermal vent mounds, and concluded that naticid gastropods were probably responsible (despite the fact that naticids are not known from such habitats). These are also likely to be the product of nematodes.

Decapod crustacean prédation on mollusks is well known, and typically takes the form of shell breaking or cracking followed by extraction of the prey. Occasionally, the prey is able to escape and repair the broken shell, leaving diagnostic shell repair scars (Fig. 10) as a sign of unsuccessful prédation (Schäfer, 1972: 408-411; Vale & Rex, 1988). Usually, the shell is fragmented; in a few cases, the predator may only effect a smaller, very irregular hole in the otherwise intact prey shell. Papp et al. (1947), provided an extensive discussion of crab prédation; subsequent authors have documented the presence of shell fragments or subsequent shell repair attributable to prédation attempts (successful and unsuccessful, respectively) by crabs and other decapods. However, because of fragmentation, one cannot account for all the remains of such prédation. Shell fragmentation may also occur because of wave action; Cadée (1968: 87-88) noted that this is usually accompanied by signs of abrasion and fragmentation in subtidal shells is probably restricted to prédation.

A most novel recent discovery is that of Norton (1988) who documented holes made in gastropod shells by a marine cottid fish, Asemichthys taylori. This species has a special set of vomeral teeth that are used to punch a hole or series of holes in the prey

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FIGS. 1-6.

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shell (Fig. 12). The holes (which are not truly "bored") allow the entry of digestive enzymes while the shell is in the digestive tract of the fish. Shells which are unpunched generally pass through undigested and emerge alive (except, of course, for limpets which have an exposed ventral aspect). Similar rows of punctures in Paleozoic brachiopods, conulariids and nautiloids were attributed to shark prédation (Mapes et al., 1989, and references therein).

Shell boring or burrowing is little known in the freshwater environment, with a few exceptions, such as the endolithic burrowing polychaete Caobangia (Jones, 1969). Recently, the Soviet paleontologist llina (1987) found shells of Unio and Viviparus (freshwater mollusks) with regular, round borehgles, one to four per shell, with an outer diameter up to 2 mm and an inner diameter from 1 .0 to 1 .5 mm. llina (1987: 29) suggested that these holes were made by ". . . ants that for reasons not yet known use their formic acid to etch perforations in the shells of molluscs . . ."; E. O. Wilson {in litt.) stated that "I don't know of any documented cases of ants boring mollusk shells, and I doubt very much if they do . . . it's hard to imagine their cutting through a clam shell even with the aid of formic acid." In any case, since ants are terrestrial, it seems unlikely that these freshwater mollusks were drilled and consumed in situ; it is more likely that empty shells were washed ashore and (post-mortem) excavated by some other organism, perhaps for a refuge. Further study is clearly indicated.

Finally, there is an extensive and scattered literature on shell borings in Paleozoic fossils. While providing lengthy descriptions of the bore holes and of the prey organisms, these studies generally have not elucidated the nature of the predator (known predatory gastropods did not evolve until the Mesozoic). Carriker & Yochelson (1968) suggested that these holes were made by soft-bodied, sessile, non-predatory organisms of unknown taxonomic affinity (this hypothesis is essentially non-testable!); Sohl (1969: 728-9) further discussed this problem. More recently. Smith et al. (1985) and Chatterton & Whitehead (1987) reviewed the Paleozoic boreholes and suggested that they were, indeed, predatory in origin although the identity of the predator remains unknown. Vermeij (1987: 176-7) hypothesized that ectoparasitic platyceratid gastropods (ecologically analogous to capulids) were the Paleozoic borers.

The remainder of this paper is restricted to analysis of prédation by naticids. The preceding review of the diversity of shell borers indicates that prédation by boring has evolved independently in a number of taxa; any similarities are undoubtedly cases of convergent evolution. The following section, on the proximate mechanisms, demonstrates the numerous unique (dehved) aspects of naticid prédation, and should be compared with what is known for other shell-boring taxa.

MECHANISMS OF NATICID PREDATION

For a detailed review and critique of the previous morphological studies on naticid feeding mechanisms, see Carhker (1981). Essentially, early controversies concerning naticid boring involved the means of boring: i.e., was it solely by mechanical means (radular rasping of the prey shell) or did it also involve chemical action (acid secretion). It was the careful work of Carriker and colleagues (Carhker, 1981) which demonstrated that the latter hypothesis is the case for naticids and muricids.

FIG. 1. Naticid bore hole (complete) in valve of Dosinia discus (Reeve, 1850) [Cocoa Beach, Florida; MCZ 145801]. Shell dimensions 52.7 mm 48.8 mm; outer bore hole diameter 5.2 mm; inner borehole diameter 2.8 mm.

FIG. 2. Naticid bore hole (incomplete) in valve of Dosinia concéntrica (Born, 1778) [Punta Guanajibo, Puerto Rico; MCZ 212607]. Shell dimensions 55.7 mm - 52.3 mm; outer bore hole diameter 2.7 mm.

FIG. 3. Muricid bore holes [presumably by Urosalpinx or Eupleura] in adjacent valves of Crassostrea virginica (Gmelin, 1 791) [Stono River, South Carolina; MCZ 226338]. Shell lengths 86 mm and 65 mm; outer bore hole diameter 2.5 mm; inner bore hole diameter 2.3 mm.

FIG. 4. Cassid bore hole in Cassidulus pacificus (A. Agassiz, 1863) [Punta Pescadero, Baja California Sur, Mexico; USNM 32907]. Test dimensions 34.9 mm • 28.9 mm, height 1 6.1 mm; bore hole diameter 2.1 mm.

FIG. 5, 6. Capulus danieli (Crosse, 1858) bore hole in valve of Comptopallium vexillum (Reeve, 1853)

[Noumea, New Caledonia; ANSP 272383]. Scallop shell dimensions 32.5 mm ^ 29.5 mm; outer bore hole

diameter 1 .75 mm; capulid shell dimensions 4.9 mm 15.0 mm.

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FIG. 7, 8. Okadaia elegans Baba, 1930 [Nudibranchia] bore hole in tube of spirorbid polychaete [Oahu,

Hawaii]. Bore hole diameter ca. 115 i^m; worm tube diameter at bore hole ca. 300 |. SEM photographs

courtesy J. D. Taylor. [Magnifications; Figure 7 at 1 10 -- ; Figure 8 at 350].

FIG. 9, Octopus bimaculatus Verrill, 1883 bore hole in Ventricolaria ford; (Yates, 1890) [Anacapa Island, off

Ventura, California; MCZ 298337]. Shell dimensions 33.7 mm -- 31 .2 mm; outer bore hole diameter 2.2 mm,

inner bore hole diameter 0.6 mm. Specimen courtesy R. F. Ambrose.

FIG. 10. Unsuccessful crustacean prédation: shell repair scars in Architectonica nobilis Röding, 1798 [Puerto

Plata. Dominican Republic; MCZ 106825]. Shell dimensions 8.8 mm y 17.5 mm.

A fundamental and little studied problem concerns the methods by which naticids detect their prey. For many predatory gastropods, chemoreception (detection of prey "chemical odors" by the osphradium) is typically the initial mechanism for determining the presence and direction of potential prey (Kohn, 1961; Croll, 1983). With infaunal naticids, the sediment habitat not only decreases the diffusion rate of chemical substances, but also may perturb its directionality; hence naticids may forage with the siphon extending to the surface where diffusion is more direct and rapid. Kitching & Pearson (1981) found that the Australian "Polinices'^ [= Conuber] incei responded to artificial sound waves directed through the substrate, which presumably mimicked the vibration of burrowing prey.

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Mechanoreception may well serve as an additional prey detection mechanism for the naticids.

Regardless of how the prey are initially detected, one can analyze the behavioral perspective: namely, recognition of suitable prey serves as a releasing mechanism which elicits a stereotyped sequence of behaviors [= fixed action patterns] (Ansell, 1960). Naticids have been little studied with respect to classical ethological principles, probably because most activity occurs while they are buried.

Edwards (1969), Schäfer (1972: 242-3), Stenzler & Atema (1977) and Hughes (1985) discussed the sequence of prey capture events: the prey is detected, evaluated, seized, covered and immobilized with copious pedal mucus, wrapped in the dilated foot of the naticid, dragged for some distance, and finally carried deep into the sand for commencement of boring.

The mechanism of naticid boring involves a complex sequence of events. There is alternate application of the predator's radula and accessory boring organ (ABO) to the bore hole site on the prey shell. The ABO is found on the ventral surface of the proboscis in naticids (but in the sole of the muricid foot); the two ABO types represent a case of convergent evolution and no homologues in other taxa are known. The ABO histology was described by Bernard & Bagshaw (1969), who characterized it as a "fungiform papilla" containing numerous epithelial secretory cells. The biochemistry of ABO secretions was discussed by Carriker & Williams (1978). The ABO secretes a complex mixture of presumed enzymes, chelators, and inorganic acid (HCl) in a saline, hypertonic solution which effects dissolution of the prey shell layers (both calcareous and organic matrix). During boring, the proboscis becomes engorged, everting both the radula and the ABO. The radula is protracted and scrapes at the surface of the bore hole. The proboscis is rotated in 90° sectors and the scraping is from the outer edge to the center, resulting in the diagnostic boss in the center of incomplete bore holes (Ziegelmeier, 1954: fig. 7; Carriker, 1981: 410). The prey shell fragments are ingested but subsequently excreted without digestion (Carriker, 1 981 : 41 1). The prey tissue is ingested by the proboscis through the borehole; Reid & Gustafson (1989) determined that external digestion does not occur.

Most studies have documented that naticids capture and consume their prey entirely within the sediment. Previous reports of naticid prédation on the sediment surface were usually a result of aquaria studies wherein the sediment depth was too shallow and consequently abnormal behavior patterns were manifested. Recently, field observations of Natica gualteriana from the Philippines (Savazzi & Reyment, 1989) have documented that this species was capable of searching for and capturing its prey on sand bars at low tide (i.e., while exposed to the air). Further study is needed to ascertain whether other naticid species can also feed on the sediment surface (exposed or subtidally). As such, this would result in greater competitive interactions between those naticids and the epifaunal muricids.

For temperate and boreal naticids, the water temperature can determine the active periods of feeding. Hanks (1953) showed that the northwest Atlantic Neverita duplicata and Euspira heros had a marked temperature-dependence, with no feeding at temperatures below 5°C and 2°C, respectively. Similarly, salinity (brackish or estuarine waters) also affects feeding rates; these two naticid species did not feed at artificial salinities below 10%o (normal seawater about 35%o).

For the calculation of energy budgets, the rates of shell boring and of prey tissue ingestion must be determined. Determining the time for infaunal prey capture and subjugation would be extremely difficult and yields variable results (here, especially, aquaria studies would be of little value). In general, the relative sizes of predator and prey (both dimensional and shell thickness) must be taken into account; there will undoubtedly be great interspecific variation in these rates. Ziegelmeier (1954) found a boring rate of 0.6 mm/day, or 0.025 mm/hour by Euspira nitida. Similarly, Kitchen et al. (1981: fig. 2) observed that in Neverita duplicata preying on various bivalves, the boring rate was a nearly constant 0.0223 mm/hour, regardless of prey species, predator size, or elapsed time. Bayliss (1986) noted that for Mya and Spisula prey, Euspira

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FIGS. 11, 12.

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alderi bored at an average rate of 0.0097 mm per hour; the prey tissue was consumed in 19.5 hours [M. arenaria), 21.5 hours (S. subtruncata), or 60 hours (S. elliptica).

For the analysis of naticid boring prédation, especially in fossils, the primary source of data for the predator is the size of the borehole. Kitchen et al. (1981: 539, fig. 4) proved that the borehole diameter is constant for a given predator size, regardless of the prey size. Most studies have used the inner borehole diameter as the basis for analysis, as this represents the size of the predator's proboscis. Wiltse (1980a: 189, fig. 1) used the diameter ". . . at the junction of the prismatic and nacreous shell layers"; this does not facilitate comparisons with other prey taxa (given that the depth of this junction is not constant for all taxa). Usually, the outer borehole diameter is also directly proportional to the predator size; but due to the chamfered borehole edge, it is more difficult to measure. However, for corbulid bivalve prey, there is an exception in that the outer borehole is disproportionately much larger than the inner borehole; this reflects the conchiolin layer in the prey shell (De Cauwer, 1985). Arua & Hoque (1989b), based solely on analysis of outer borehole sizes, concluded that the opening was more oval than circular; regrettably, their data on inner borehole sizes was not presented.

It is unfortunate that a recent paleoecological study (Arua & Hoque, 1989a, 1989c) seems to have confused several muricid boreholes with those of naticids, and vice versa. Their "hole types" A, and D were claimed to be muricid; C, E and F as naticid. The authors had stated that naticid boreholes are countersunk, with tapering sides, and incomplete ones have a central boss; yet, they claimed that their "hole type E," which lacks a boss and has vertical sides, was naticid! My re-analysis of their descriptions leads to the conclusion that their "hole types' E and (maybe) A are muricid; whereas B, C, D, and F are naticid. This confusion undoubtedly has arisen in other studies, and should be considered when interpreting community-level analyses (because the variety of observed boreholes are rarely illustrated therein).

A more general aspect of naticid prédation is the suitability of the substrate for naticid locomotion. It is well known that naticids are restricted to infaunal sedimentary habitats; it is less appreciated that extremely fine or smooth grained substrates (silt-mud-clay) are precluded because they are too tightly packed to burrow through readily, in contrast to coarser sand substrates (Yochelson et al., 1983: 12; Maxwell, 1988: 31).

Vermeij (1980) and Ansell & Morton (1987) discovered that the tropical Polinices "tumidus" [= mammilla], after wrapping its prey in a mucus coat within the foot, retained the prey until suffocation and gaping occurred.

Subsequently, the prey was consumed without boring. Ansell & Morton (1987: 117) suggested that a "narcotizing toxin" may play a role in causing prey gaping, such as by thaidine gastropods preying on barnacles. This was questioned by Reid & Gustafson (1989), who determined that prey suffocation alone caused shell gaping. The ecological and evolutionary implications of this non-boring prédation will be discussed below.

A preposterous view of the evolution of naticid feeding mechanisms was advanced by Stafford (1988), who claimed that naticids originated at Ediacaran-Cambhan times (570 million years ago), as swimming filter feeders, and gradually shifted to benthic feeding entailing eversión of the stomach (as in asteroids) to effect external digestion of the prey.

To summarize the proximate mechanisms of naticid shell boring: (a) Prey are detected by chemoreception using the osphradium, though mechanoreception may also play a role, (b) Suitable prey are seized, covered with pedal mucus and wrapped in the foot, (c) The proboscoideal acid-enzyme secretory accessory boring organ (ABO) together with the radula is used to excavate a countersunk (bevelled) hole in the prey shell, and the prey tissues are extracted through this borehole. The size of the borehole (inner diameter) is

FIG. 11. Aegopinella nitidula (Draparnaud, 1805) [Zonitidae] bore holes in (left) A. pura (Alder, 1830) [bore hole 1.5 mm 0.7 mm] and (right) A. nitidula [bore hole 1.6 mm 1.0 mm] [Monks Wood, England]. Photographic negative courtesy P. B. Mordan; original in the Biological Journal oí the Linnean Society (1977), 9: 65, plate 1A. [Copyright 1977 by The Linnean Society of London].

FIG. 12. Asemichthys taylorl Gilbert, 1912 [Pisces], punched holes in Margante sp. [San Juan Island, Washington]. Shell width ca. 2 mm. Maximum hole diameters: 165 |; 350 |.: 380 fj.m. SEM negative courtesy S. F. Norton; original in Science (1988), 241(1): cover. [Copyright 1988 by the AAAS].

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positively correlated with predator size, (d) Some tropical Indo-Pacific naticids are able to immobilize their bivalve prey until shell gaping occurs, allowing direct access to the prey tissues; thus, no borehole need be made.

THE PREY OF NATICIDS

The Appendix tabulates the known prey of naticid gastropods (fossil and Recent). The genera are arranged alphabetically by family; the reference is given in brackets following the species name [n.b. this is not the author of the taxon!]; some species were reported in several studies but only one such is indicated herein. This compilation includes an unpublished data set on Fijian Pleistocene mollusks collected by A. J. Kohn. I have corrected for obvious changes in generic nomenclature; species names were not given for several reports, as indicated by an asterisk. Many records of naticid prédation are purely incidental or even parenthetical (e.g., "by the way, some of the shells of X were bored . . ."), which does not facilitate critical comparative analyses.

Generally, the records herein are limited to ecological or paleoecological studies emphasizing prédation; it is too time-consuming to search through the general systematic and faunistic literature for scattered records of naticid prédation (which are usually not thoroughly documented in such papers). Needless to say, aquarium studies of naticid feeding should be based on prey found in the same habitat as naticids. Unfortunately, some papers (Hayasaka, 1933; Fischer, 1966; Sander & Lalli, 1982; and De Cauwer, 1985) provided lists of taxa with gastropod boreholes, but without specifying naticid or muhcid boreholes. Nonetheless, based on the available data, it appears that naticids prey on the majonty of benthic, infaunal shelled mollusks.

A. Class Gastropoda

Since most archaeogastropods (e.g. Pleurotomaroidea, Fissurelloidea and Patelloidea) are rocky-habitat dwellers, they are not subject to naticid prédation. Beebe (1932; 212, fig.) made the unusual statement that, in Bermuda, Natica canrena preyed upon the rocky intertidal limpet Fissurella barbadensis. leaving a diagnostic borehole in the limpet shell. My subsequent re-analysis of this situation reveals that Beebe had confounded the excurrent slit or foramen ("keyhole") of these limpets with naticid boreholes and erroneously assumed that naticid prédation was responsible for the limpet keyholes!

Many of the soft-substrate taxa in the Mesogastropoda are subject to naticid prédation. Not included herein are the extensive reports of confamilial prédation on naticids themselves (sometimes referred to as "cannibalism") (Kabat & Kohn, 1986). Reports of naticid boreholes in Xenophora [Xenophoridae] and Lamellaria [Lamellariidae] by Adegoke & Tevesz (1974) are questionable, given the epifaunal habitat of these taxa. While it may appear that neogastropod genera are more frequent in the list, this could be a taxonomic artifact of generic lumping vs. splitting.

Most of the neogastropods are active predators themselves; the epifaunal and rocky-habitat species generally escape naticid prédation. It is entirely possible that some of these records, especially of Muhcidae, are of misidentified muricid boreholes.

B. Class Bivalvia

Most infaunal bivalves are subject to naticid prédation. In particular, the venerids, tellinids, and lucinids (the last two often with relatively thin or little-sculptured shells) are frequent victims. The infaunal Solemyidae live in reducing sediments where naticids are not found. Bivalve taxa that are in rocky habitats, epifaunal byssate or cemented (Dimyoidea, Plicatuloidea, Anomioidea, Chamoidea, Leptonoidea and Cyamioidea) effectively escape naticid prédation; the few cases of naticid boreholes in the Pterioidea, Limoidea, Ostreoidea and Pectinoidea are unusual exceptions. Those that are rock or wood burrowers (Lithophagidae, Gastrochaenoidea and Pholadoidea) are also inaccessible to naticids. The Pinnoidea and Tridacnoidea have encrusted and sculptured shells; the Glossoidea, Clavagelloidea and Pholadomyoidea are too rare to have been reported in this context.

Class Scaphopoda

A thorough review of naticid prédation on scaphopods by Yochelson et al. (1983) found that scaphopods were the occasional prey of naticids from the Late Cretaceous to the Recent. Usually, there is moderate stereotypy of borehole siting, with most being laterodorsal

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and about midway along the shell axis. It was found that coarse-ribbed scaphopods (which live in coarse sediments) were much more likely to be bored; those with smooth (or no) ribs, living in fine sediments, escaped naticid prédation by virtue of their habitat which is inimical to active naticid burrowing (Yochelson et al., 1983).

D. Other Mollusk classes

Naticid prédation has not been recorded on the Aplacophora, Monoplacophora, Polyplacophora, or the Cephalopoda. The shell-less Aplacophora would not leave traces of naticid prédation. The Monoplacophora (clay-mud habitats) and the Polyplacophora (rocky habitats) are usually not encountered by naticids. The epifaunal and pelagic cephalopods, predators themselves, are unlikely to be captured by the slower naticids.

E. Polychaetes

Paine (1963: 69) found one specimen of Neverita duplicata from Florida that fed on the polychaete Owenia fusiformis; this is the only known record of naticids preying on annelids. It is not clear whether this represents normal behavior or a single, aberrant event.

F. Crustaceans

Significantly, Conor (1965: 229) found that naticids would not feed on hermit crab occupied shells. This is of importance as it indicates that not only can naticids recognize such "prey" (of course, the active epibenthal hermit crabs may be beyond the range of naticids), but also that boreholes found in shells with recognizable signs of hermit crab occupancy (worn lips, unrepaired damage, epibionts) were the cause of the gastropod mortality, freeing the shell for hermit crab use.

Ostracods represent a potentially important prey source for juvenile naticids. Livan (1 937) and Reyment (1966, 1967) attributed numerous boreholes in ostracods to predatory gastropods. Maddocks (1988) reviewed the various types of boreholes in ostracods (Cretaceous to Holocene of Texas) and concluded that juvenile naticids were responsible for most. However, because of the thin ostracod test, there is a wide variety of "holes" and it is difficult to attribute them to known causes (Reyment et al., 1987).

G. Brachiopods

Most articulate brachiopods live in rocky habitats (rock walls or boulder grounds), thereby escaping naticid prédation because of habitat incompatibility. However, Witman & Cooper (1983: 71, figs. 8c-<l) reported "naticid" boreholes in values of Terebratulina septentrionalis from the Gulf of Maine, which they attributed to either Natica clausa or N. pusilla. The illustrated boreholes resemble those of muricids (albeit with slightly sloping sides); further study is recommended.

H. Pisces

Perry (1940: 116) reported that the tropical western Atlantic Naticarius canrena "preys on bivalves and has been seen to devour dead fish." This remarkable observation, if true, represents the only known record of piscivory in the Naticidae. However, if it is based on aquarium observations, then it may simply reflect aberrant behavior by starved individuals (see the next paragraph).

I. Scavenging

Most studies have shown that naticids will only feed on fresh prey; carrion-feeding (as in the neogastropod Buccinidae and Nassariidae) is not manifested. A few studies (typically in aquaria) have shown that gaping (dying) bivalve prey may be consumed directly without boring (Ansell & Morton, 1985). It is not clear if this laboratory behavior is also shown in the field.

J. Egg Capsules

Several authors have reported "naticid" boreholes in the egg capsules of various deep-sea organisms. These observations include Thorson (1935: 12-13, figs. 4a-c) in egg capsules of the neogastropod buccinid Sipho [= Colus] curtus from East Greenland; Jensen (1951, fig. 1) in egg capsules of the ray (Rala) from Davis Strait (the boreholes ranged from 0.75 to 2.5 mm in diameter; a few capsules had multiple boreholes); and Ansell (1961) in egg capsules of the dogfish (Scylliorhinus canícula) with countersunk boreholes. It must be emphasized that naticids were not observed boring these holes; these authors had merely conjectured that naticids were the most likely causative agents. These boreholes were clearly effected from the outside (i.e., they are not the hatching-out holes of the juveniles within). First, for the buccinid egg capsules, it is probable that a muricid bored the holes, as is known for some other muricids (Abe. 1985). Second, for the elasmobranch egg cases, a more likely predator is the unusual deep-sea archaeogastropod family Chohstellidae, which are typically associated with skate egg capsules upon which they feed (Hickman. 1983: 86).

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The pnmary prey sources for naticids are infaunal gastropods and bivalves. The data [Appendix] document that 47 gastropod families (out of 129 shelled marine gastropod families) and 35 bivalve families (out of 109 marine bivalve families) are known to be subject to naticid prédation. The major gastropod prey sources are the Turritellidae and Naticidae (Mesogastropoda) and the Turhdae (Neogastropoda). The major bivalve prey sources are the Lucinidae, Tellinidae and Veneridae (Heterodonta).

FOSSIL RECORD OF NATICID PREDATION

This section tabulates the reports of fossil naticid prédation and is arranged by geological time period. In general, only bnef summaries are provided; discussion of any broader ecological aspects is deferred to the following section in combination with related conclusions from Recent studies. It must be emphasized that it is difficult to track down all the paleoecological studies, especially those that are "buried" within lengthy systematic monographs (no attempt has been made to search through the latter). Indeed, it seems better that extensive paleoecological researches should be published separately from narrower taxonomic studies, in order to bring them to wider notice.

A. Tnassic

Fürsich & Wendt (1977: 299) mentioned "naticid" boreholes from the Cassian Formation of northern Italy (Tirol). Subsequently, Fürsich & Jablonski (1984) illustrated the boreholes, showing the diagnostic countersunk appearance of incomplete boreholes, and discussed the implications thereof. The bivalve prey were Cassianella and Palaeonucula:\he gastropod predators were referred to several species of the naticid genus "Ampul-

Una" Newton (1983; Newton et al., 1987: fig. 25.2) independently documented "naticid" boreholes in the epibyssate limid Mysidioptera from the Wallowa Terrane of the Hells Canyon (Oregon-Idaho); this suggests that the Triassic borers were somewhat widespread, before becoming extinct. However, the taxonomy of Triassic "naticids" remains a morass, and their familial assignment is still uncertain. Further discussion of the evolutionary consequences of Triassic boring préda-tion is deferred to the next section. Indeed, if these countersunk Triassic boreholes are not those of naticids, then it remains uncertain whether all the younger occurrences of countersunk boreholes are correctly atthbuted to naticid prédation.

Sohl (1969: 726) expressed some doubt as to whether the Tnassic forms were true naticids; in any event, his spindle diagram of naticid clade diversity (his fig. 1) clearly shows that from the Triassic to the mid-Cretaceous, there are never more than five genera in any epoch; naticid diversification did not commence until the Upper Cretaceous, with the evolution of the bohng habit. Bande! (1988: 270) claimed that "Thus Tnassic naticids,' to a large extent, are neritoideans, some belong to other groups, but none appear to be naticids"; this needs further documentation.

B. Jurassic

Sohl (1969: 729) searched through vahous paleontological monographs and collections of Jurassic mollusks and found no signs of molluscan boreholes. Fürsich & Jablonski (1 984) also concluded that there were no gastropod borers in the Jurassic.

Cretaceous

Fischer (1962a) reviewed some reports of Cretaceous boreholes and attributed most to naticids, as there were relatively few muricids at that time. Subsequently, Sohl (1969: 731) more carefully analyzed Cretaceous boreholes and found a few from the Cenomanian (100 myr) and a much greater abundance from the Campanian (75 myr). The Ripley Formation (Campanian) was studied in greater detail by Vermeij & Dudley (1 982) who also found extensive shell repair and a size refuge from boring prédation. The oldest Cretaceous records were shifted further back by Taylor et al. (1983) who documented naticid prédation from the Blackdown Greensand of England (Alblan, 105 myr). They found that the vast majority (92%) of boreholes were naticid, with a nearly equal ratio of gastropod to bivalve prey (in contrast to the few muricid boreholes, found primarily on bivalve prey).

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The diversification of naticids (and other modern marine families) at this time represents the "Mesozoic marine revolution" of Vermeij (1977), and is discussed in the next section. Vermeij & Dudley (1982) reported no prédation on naticids in the Ripley Formation (Tennessee); subsequently, Kitchell et al. (1986: 293, fig. 1h) found a multiple-bored specimen of Euspira rectilabrum. from the same outcrops. This is the earliest record of confamilial naticid prédation in the fossil record.

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D. Paleocene

I have not found any paleoecological studies from the Paleocene reporting on naticid boreholes. Naticids were present then; future studies of these faunas would be most worthwhile.

E. Eocene

Fischer (1960, 1962a, 1963) reported on naticid prédation in the Lutétien Stage of France and found that for the bivalve Petunculus [= Glycymehs], 4.6% of the specimens were bored, primarily the smaller ones. For the gastropod Mesalia. 70.9% were bored by naticids (of which only 7.7% were incomplete holes), and some had multiple complete or incomplete boreholes. For Corbula spp., there was a rather high rate of boring failure (to 26% of the specimens). This fauna was also analysed by Taylor (1970) who found numerous naticid and muricid boreholes and an overall confamilial naticid prédation rate of 1 1 .3%.

Siler (1965) briefly reported on the Gosport Formation of Texas and found both naticid and muricid boreholes on the bivalve Lirodiscus tellinoides. A more comprehensive study on the Stone City Formation of Texas (Stanton & Nelson, 1980; Stanton et al., 1981) recorded a naticid mortality rate of 15% and a crustacean mortality rate of 20% for molluscan prey. The latter studies entailed considerable efforts to reconstruct the food web and paleocommunity structure.

Several studies were carried out on the Ameki Formation of Nigeria by Adegoke & Tevesz (1974), Arua (1989) and Arua &

Hoque (1987, 1989a, 1989c). They found that turrids and terebrids were the preferred gastropod prey; the latter authors also found extensive prédation on bivalves. However, as discussed eartier, some of the boreholes seem to have been misidentified (vis á vis naticid vs. muricid) by Arua & Hoque. An analysis of bivalve prey {Arcopsis and Limopsis) from the Pallinup Siltstone in Western Australia found that 9.2% of the bivalves had gastropod boreholes, one fifth naticid and four fifths muricid (Darragh & Kendrick, 1980).

F. Oligocène

Klähn (1932) analyzed naticid prédation on other naticids from the Sternberg Formation of Germany and found high prédation rates from 53.3% (the second smallest prey size class) to 15%-26% (the other classes); the documentation provided does not facilitate further analysis.

G. Miocene

Hoffman et al. (1974) conducted an extensive study on the Korytnica clays of Poland and found a confamilial naticid prédation rate of about 10%; unfortunately, their data (table 1) do not fully partition the boreholes by naticid or muricid sources. Subsequently, Hoffman (1976a) attributed most of the bivalve mortality to sedimentation, rather than préda-tion; similarly, abiotic factors accounted for much of the gastropod mortality (Hoffman, 1976b). Other Miocene outcrops from Poland were studied by Hoffman & Szubzda (1976), primarily with respect to food webs and community structure. Kojumdjieva (1974) studied the Tortonian and Sarmatian outcrops of Bulgaria and found a variety of naticid and muricid prey taxa; very few unsuccessful or multiple boreholes were observed.

Thomas (1976) analyzed naticid prédation on glycymerid bivalves from various Neogene (Miocene-Pliocene) outcrops in the eastern United States and concluded that prédation rates in the Miocene were comparable to those on Recent glycymerids; however, the size-selectivity data seemed questionable. This research was reanalyzed by Kitchell et al. (1 981 : 545-548), who determined that the seemingly contradictory results of Thomas could be explained by the fact that there were actually two different naticid predators (of markedly different sizes) in the various fossil faunas; this meant that the observed "changes" in preda-

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tion intensity or prey size were merely an artifact of wfiich naticid predator was present.

A series of studies on the Chesapeake Group of Maryland was conducted by Kelley (1982a-1989b). with an emphasis on bivalve prey. Nearly three-fourths of the mortality could be attributed to naticid prédation; for some prey there was an increase (over geological time) of prey size and shell thickness. This was hypothesized to be an evolutionary response to naticid prédation. Dudley & Dudley (1980) made a briefer analysis of boring prédation on three mollusk species from these outcrops, and observed a size refuge from prédation for the two bivalves studied.

Cotbath (1985) reported on the outcrops of the Astoria Formation of Oregon and noted extensive naticid prédation, primarily of bivalves; other prédation sources were not analyzed. The Wimer Formation of northern California was analyzed by Watkins (1974), who found low levels of naticid prédation on several bivalves.

Maxwell provided a thorough systematic and paleoecological analysis of the Stillwater Mudstone of New Zealand and observed considerable naticid prédation on various gastropods and bivalves. The data were used to reconstruct food webs (Maxwell, 1 988: 34, fig. 3) as part of an overall trophic analysis which also considered non-fossilized aspects of the community. There was extensive confamilial naticid prédation, especially of the smaller-sized species. This monograph is an excellent model of integrating systematics with paleocommunity reconstructions.

H. Pliocene

Boekschoten (1967) studied the fauna of the Tielrode Sands of Belgium and reported some confamilial naticid prédation, although crustacean prédation was a far more important source of mortality for the naticids. The

Emporda of Spain was analyzed by Hoffman & Martinen (1984), who observed high selectivity in prey size and borehole site choices. Guerrero & Reyment (1988b) used multivariate analysis to differentiate between naticid and muricid boreholes in Chlamys from the Lower Pliocene near Malaga, Spain. Robba & Ostinelli (1975) analyzed gastropod, cephalopod and crustacean prédation in the Albenga outcrops of Italy and noted that 13.9% of all specimens were bored, nearly all by naticids. Hingston (1985) reported on the Muddy Creek assemblage from Victoria, Australia,

and determined that about 75% of the boreholes were naticid and the remainder muricid; edge drilling of bivalves was rare, and prey shell sculpture resulted in a greater frequency of unsuccessful boreholes.

I. Pleistocene

Kabat & Kohn (1986) analyzed prédation on naticids from the Nakasi Beds of Fiji and observed rather high naticid prédation rates on Natica spp., but considerably lower confamilal prédation on species of Polinices and Sinum. Unsuccessful crustacean prédation was quite common; successful crustacean prédation probably accounted for a greater amount of mortality than did confamilial prédation. Berg & Nishenko (1975) found that 26% of the shells of Nassarius perpinguis from the San Pedro deposits of California showed naticid boreholes; stereotypy of borehole siting was shown, although no data on predator or prey sizes were given. A much more detailed analysis of the nearly contemporaneous Puerto Libertad deposits of Sonora, Mexico, and a thorough trophic web reconstruction was conducted by Stump (1975: fig. 18).

J. Sub-Holocene

Yochelson et al. (1983) analyzed naticid prédation on scaphopods from the elevated "mud lumps," or diapir structures from the Mississippi River delta (ca. 15,000 years old), and found (in two large samples) that almost 58% of Dentalium laqueatum had boreholes. They noted that other scaphopod assemblages (fossil and Recent) showed far fewer naticid boreholes (usually less than 1 0%); this assemblage undoubtedly reflected exceptional naticid feeding.

Since the end of the Early Cretaceous (Albian), naticid prédation has been documented through Holocene faunas (except for the Paleoceno), although probable naticids are known from the Jurassic. Potential "naticiform" boreholes from the Thassic are known; the evidence is not conclusive as to whether or not the Triassic predators actually were naticids. The available data do not show any clear trends in the rates of gastropod boring prédation since the Cretaceous (Vermeij, 1987: fig. 7.6); however, comparisons between assemblages should be based on ecologically analogous taxa, and studies of a single prey family need to consider possible changes in defense mechanisms (especially shell form) over time.

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Another area of interest is the use of bore holes in the field of ichnology, or the study of trace fossils. Most paleontologists recognize animal locomotory tracks as trace fossils; however, this field includes any and all remains of the activities of living organisms. Thus, a borehole found in a fossil specimen is, per se, a trace fossil, and can be described and discussed in the absence of exact knowledge of the causative agent. Needless to say, there has been some controversy over the "nomenclature" of trace fossils; the International Code of Zoological Nomenclature (ICZN, 1985; Articles Id, lOd, 42b) currently does recognize "ichnotaxon names," as a parallel nomenclatural system. Hantzschei (1 975), Warme & McHuron (1 978) and Ekdale et al. (1984) provided excellent reviews of trace fossils.

Predatory boreholes in fossil specimens can be referred to the ichnotaxon "Praedichnia" Ekdale, 1985; those produced specifically by mollusks to the ichnotaxon "Oichnus" Bromley, 1981; and those identical with naticid boreholes to the ichnotaxon "Oichnus paraboloides" Bromley, 1981. Maddocks (1988; 641-2) "arbitrarily defined" 20 "ichnophena" corresponding to different forms of boreholes in ostracod tests; this diversity is unrealistic and meaningless. These names have no heuristic value; if they can be attributed to a known predator, then they should be referred

to as "borehole of ", whereas those of

unknown predators should not be given formal names.

ECOLOGICAL ASPECTS OF NATICID PREDATION

This section attempts to integrate and synthesize, from an ecological perspective, the vahed aspects of naticid prédation. It is hoped that this will not only indicate what has been well documented but also reveal promising (or neglected!) areas for future research. I have not attempted statistically to re-analyze previous studies or to provide detailed criticisms of previous methodologies, unless it seemed directly warranted. Subsequent researchers would be well advised to re-check the relevant previous studies. My section on

"Mechanisms of naticid prédation" above included the more proximate aspects of naticid prey detection, capture and boring; this section covers the broader, ultimate aspects of naticid prédation, as well as several topics from the "prey's viewpoint."

A. Prey Size and Species Choice

The embryos of naticids feed on dissolved organic matter (DOM); some species have yolk reserves or infertile nurse eggs which serve as additional food resources, especially for those with direct development. Naticid species with planktotrophic larvae feed on the phytoplankton while in the swimming stage; those with lecithotrophic larvae undoubtedly rely on DOM in addition to their yolk reserves (Ansell, 1982c).

The feeding habits of juvenile naticids have been much less studied. For example, Ansell (1982c) reported that they ate various unspecified gastropods or bivalves of small size; Berg (1976) was able to feed them Bittium and Rissoella, although this was limited to aquarium studies. Wiltse (1980a) found that juvenile Neverita duplicata at Barnstable Harbor (Massachusetts) consumed the diminutive venerid Gemma gemma: because of the high density of the latter, naticid prédation accounted for less than 15% of total prey mortality. Maddocks (1988) concluded that juvenile naticids represented significant predators of ostracods; with ontogeny, the naticids shift to larger-sized molluscan prey.

Adegoke & Tevesz (1974; 22) claimed that "no direct correlation was found between prey size and predator size"; but no statistical data were presented to support this statement. Other studies, however, have shown that there is usually a good correlation between predator size (as determined by the inner borehole diameter) and the prey size (e.g Ansell 1960; Baytiss, 1986; Griffiths, 1981 Kabat & Kohn, 1986; Kitchell et al., 1981 Macé, 1978; Martineil & De Porta, 1982 Robba & Ostinelli, 1975; Selin et al., 1986 Wiltse, 1980a). Colbath (1985) reported little correlation between borehole diameter and prey size, except for Katherinella prey. However, these results are a consequence of Colbath's use of bivalve shell "width" rather than the more conventional length as the dimensional measure.

Also of importance is the relative size of the prey taxa and the naticid predators. Large prey species are often less susceptible to pre-

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dation by naticids than are small prey species. Similarly, within a species, smaller individuals usually suffer greater naticid mortality (e.g. Franz, 1977; Jackson, 1972). Penney & Gnffiths (1984) used three-dimensional prédation contour diagrams to display the relationships between predator size, prey size, and quantity of prey consumed. Alternatively, Hoffman (1976b: 296) showed no size-selectivity for some (but not all) gastropod prey from the Poland Miocene. However, Green (1968) found that mortality from naticid boring of the bivalve Notospisula parva actually increased with prey shell size; similar results were shown by Mukai (1973) and Wilson (1988). As discussed below, increased prey size over geological time may represent an evolutionary response to naticid prédation (or is of adaptive value to escape prédation) (Kelley, 1984, 1989b).

Prey switching, or prey choice, has been a contentious point; the fundamental question of "why" a given naticid will pick a certain prey species given an equal choice of several species can lead to teleological explanations. Ansell (1983) found that dietary switching will not occur and suggested that "preconditioning" may play a rôle in species choice. Broom (1 983) found that younger Natica maculosa fed on Pelecyora trígona. whereas older predators fed on Anadara granosa: ontogenetic dietary switching thus occurred.

Several studies, using a variety of prey items, have determined a hierarchy of preferred prey choices. For Euspira alden. Bayliss (1986; 40) found that the preferred bivalve prey, in descending order, were; Mya. Spisula. Cerastoderma and Parvlcardium: Árctica and Corbula were not preyed upon. Similarly, George (1 965) found that mortality due to naticids was most prevalent in Glycymens glycymeris, and less so in Donax semistnatus and D. trunculus (the latter the larger species). Kitchen et al. (1981) found that for Neverita duplicata, the preferred prey, in descending order, were; Mya. Mercenaria. Mytilus and Neverita. Although Neverita was actually the highest in energetic value, the handling costs were such that only much smaller conspecific prey could be captured by the naticid predator, Kelley (1 989a) found that bivalve prey from the Maryland Miocene were preferentially bored, in descending order, as; Eucrassatella. Anadara. Astarte (the latter two roughly equivalent) and Corbula. with slight differences from one formation to another.

The same naticid species, in different localities, may have markedly different diets. Thus, Natica maculosa in Penang (Malaya) feeds wholly on gastropod prey, especially the trochid Umbonium vestianum. whereas this species at Kuala Selangor (Sumatra) feeds on bivalve prey, particularly Anadara granosa. In this case, it is the relative availability of prey taxa which determines (in part) the diet of a given naticid species (Broom, 1982; Berry, 1982).

A recent series of studies by Kitchell and colleagues (Kitchell et al., 1981 ; DeAngelis et al., 1984, 1985, 1989) have attempted to model the energetic and coevolutionary aspects of naticid ecology. The first study was of value in providing a useful model for the testing of naticid prédation; however, the subsequent papers incorporated multiple assumptions which decreased their representation of the real world into a senes of parameters couched in advanced equations. This reductionist approach cannot account for complex, stochastic, and hierarchial ecological communities.

It is worthwhile to elaborate briefly the basic pnnciples of the Kitchell models. Essentially, the cost;benefit ratio for various prey species is determined (costs being the time and energy to recognize, capture/subdue, bore, and digest the prey; benefits the energetic value or gain of prey tissues) and related to both prey size and predator size, given that the cost of a specific prey will vary according to the predator size. From this, one can graphically represent the cost-benefit functions with prey size as the dependent variable and cost; benefit ratios as the independent variable. The lowest curve represents the optimal prey choice. These curves show that optimum prey are of intermediate sizes; too-small prey are of low energy value and too-large prey can usually escape the predator. Kitchell (1987) found that these models lead to the prediction that "larger naticid predators should be more highly selective than smaller-sized naticids," all other factors being equal. Discussion of their later models, dealing primarily with predator-prey coevolution has been deferred to section F, under the evolutionary aspects.

Kelley (1982b, 1987, 1989a-b) used these methods to analyze naticid prédation in the Maryland Miocene fauna, and confirmed that the models predict prey selection patterns, but with some exceptions. She found that over time, bivalve prey shell thickness (= cost) increased while there was no overall

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trend in shell volume (= benefit). Commito (1987) questioned the validity of the Kitchell models and noted that their assumptions neglected several important factors with respect to prey defense strategies (or adaptations): ignored were the possibilities of depth refuges, shell ornamentation, chemical defenses, or behavioral responses, all of which could deter naticid prédation. DeAngelis et al. (1987) acknowledged these criticisms and suggested that yet further modelling would be able to incorporate these aspects of prey biology. It is difficult to account fully for all the parameters or variables that determine or influence prédation processes; any model that attempts to do so would likely be so unwieldy or incomprehensible as to be of little heuristic value.

Interestingly, Ansell (1982b) found that Euspira alderi would not feed on opened bivalves — only live, closed prey items were chosen. These same results were found by Kitchell et al. (1986: 297) for Neverita duplicata. This suggests that the stereotypy of prey choice restricts the naticids to fresh prey, and rules out scavenging or carrion-feeding.

Prédation by naticids on other naticids can be quite widespread and represents a significant source of naticid mortality. Although occasionally referred to as "cannibalism," that term is inappropriate since this prédation does not necessarily involve conspecifics. Studies from the Nigerian Eocene showed that about 15% of naticid shells had naticid boreholes (Adegoke & Tevesz, 1974); Colbath (1985) observed only 2.7% such in the Oregon Miocene; Hoffman et al. (1974) noted 10% such in the Poland Miocene. Boekschoten (1967) found that 7.8% of the naticids from the Belgian Pliocene had naticid boreholes. Kabat & Kohn (1986) determined that in the Fijian Pleistocene, naticid prédation on Natica spp. accounted for 27% of mortality, whereas that on Polinices and Sinum spp., for only 3% of mortality. The latter genera have more globose shells and a larger foot which may provide faster locomotion and hence facilitate escape from confamilial predators. Maxwell (1988) concluded that smaller-sized naticids of the New Zealand Miocene had much higher naticid prédation rates, confirming size-selectivity aspects of naticid prédation. Several studies on Recent naticids have also shown extensive confamilial prédation (Burch & Burch, 1 986; Fretter & Manly, 1 979). Obviously, there is considerable variation as to the extent of confamilial naticid prédation;

disease and prédation by fish or crustaceans may represent more important naticid mortality pressures.

B. Stereotypy of Boring on Prey Shell

For gastropod prey, there has been some confusion among studies with respect to the siting of successful boreholes, with some "results" actually of no consequence. Thus, Arua & Hoque (1989a: 55) emphasized that the "preferred drilling site" on the apertural side was on the last whorl; however, because of whorl overlap, most of the exposed prey shell surface is the last whorl, and thus purely non-random borehole siting would lead to most boreholes located there (their other results combine 1 1 prey species into a single table which does not facilitate further analysis). Yet, for some gastropod prey, there is a predominance of prédation on the dorsal (abapertural) side over the ventral (apertural) side; this reflects the increased ability of the prey to escape in the latter position (Adegoke & Tevesz, 1974). However, other studies suggested that prédation on the ventral side is preferred since the predator's foot seals off the aperture, blocking escape (Berg, 1976: 3; Berry, 1982). Some studies have shown that certain gastropod prey are preferentially bored on the penultimate whorf (rather than the last whorl); this, too, reflects prey handling factors (Dudley & Dudley, 1980; Hoffman & Martinen, 1984). Boreholes that are at either extreme end (apical or abapical) may not allow the proboscis to penetrate the entire shell; more centrally located boreholes may facilitate complete consumption of the prey tissues.

For gastropod prey, it is convenient to analyze the stereotypy of borehole siting by the various geometrical subsets of the shell. Not only can one distinguish between the outer (body) whorl and the older, apical whorls [i.e. the horizontal dimension], but one can also partition the prey gastropod shell whorts into semicircular sectors, or longitudinal zones [i.e. the vertical, or axial dimension]. Thus, Berg (1976) and Berg & Nishenko (1975) developed two conflicting numbering schemes for the latter division. In the 1975 paper (their figure lb), the sectors (numbered 1-8) started with the apertural plane and proceeded counterclockwise (when viewed from the apex); thus, their clockwise "pie chart" (their figure 1c) of the sectors is actually viewed abapically. But, in the 1976 paper (his

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figure 2a) the sectors (also numbered 1-8) started with the apertura! plane and proceeded clockwise (when viewed from the apex); their clockwise "pie chart" (his figure 2b) is, this time, viewed apically! It is not clear what has been done here: my recommendation is that future investigators explicitly specify which scheme they are using.

Kabat & Kohn (1986: fig. 4), using the first scheme, observed that for naticid prey, boreholes were found in four of the eight shell sectors, with nearly 90% occurring in two 90° sectors: however, there was little overall evidence for stereotypy of borehole siting. Robba & Ostinelli (1975: 327) independently depicted an angular measurement system which corresponds to the first scheme of Berg. Stump (1975: figs. 19-21) devised an elaborate "equal-area projections" system to show frequency-contours (in percentages) of borehole siting on the various prey shells.

Regrettably, this method is difficult to visualize and does not lend itself to comparison with the other, more direct schemes: it does not seem to have been used by subsequent authors.

Some studies have shown that most boring occurs near the shell margin of bivalve prey, where the shell is thinner and there is no sculpture (e.g., Ansell, I960: Ansell & Morton, 1985). Other studies, however, have shown a preference by other naticids for boring near the umbones (e.g. Ansell & Morton, 1985: Arua & Hoque, 1 989: Bernard. 1 967: Colbath, 1 985: George, 1 965: Jacobson, 1 968: Kitchell et al., 1981: Leidy, 1878: Matsukuma, 1976: Negus, 1975: Rieron, 1933; Thomas, 1976; Vignali & Galleni, 1986): or in the mid-region (Bayliss, 1986: Griffiths, 1981; Vermel) et al., 1989). The strongly inequilateral Periploma margaritaceum was primarily bored on the anterior slope, due to its shell form (Rosewater, 1980). Some earlier studies had suggested that naticids preferentially bored near the prey gonads or digestive tissues (Pelseneer, 1924; Verlaine, 1936); however, borehole siting is primarily a function of the manipulation of the prey dunng boring and may depend on the prey shell morphology. In a few cases, little stereotypy is manifested. Berg & Porter (1974) found that, for the same bivalve prey, there were significant differences between naticid species as to the preferred borehole position; Berg (1975) suggested that behavioral differences in prey capture and handling influenced species-specific patterns.

Probably of greater importance are (1) the size of the prey relative to the predator; (2) the shell thickness and presence or absence of sculptural elements; (3) the relative convexity of the prey shell: (4) other factors relating to the predator's manipulation of the prey. Based on this review, no one element solely determines the locus of borehole siting among bivalve prey.

The majority of studies have shown little preference for right vs. left valves of bivalve prey, as would be expected given the equivalve nature of most infaunal bivalves. Some studies have shown 10-20% "differences" in the frequency of boreholes between valves, but no clear trends are apparent. Needless to say, for each valve with a borehole, there is a matching, unbored valve; hence the naticid mortality rate is twice the number of bored valves divided into the total number of valves. It is incomprehensible as to what Lever et al. (1 961 : 341) meant when they stated that "the percentual mortality may in some cases exceed 100 [%]."

Adegoke & Tevesz (1974) stated that Varicorbula from the Nigerian Eocene was pleurothetic and invariably bored on the right valve which is closer to the surface. However, as noted below, the left valve of corbulids has a thick periostracum which deters boring prédation; the position of the corbulid shell in the substrate is of less import (De Cauwer, 1985). More generally, since naticids usually manipulate their prey prior to boring, the life position may be of little relevance. Newton (1983) found that the Thassic limid Mysidioptera was always bored through the left valve; this taxa is an epibyssate recliner and the left valve is adjacent to the substrate (Newton et a!., 1987: fig. 27).

Incomplete and Multiple Boreholes; Non-boring Prédation

Incomplete boreholes are usually interpreted to represent a sign of interruption of prédation, whether by prey escape, arrival of another predator, or other disturbance. In some cases, the same naticid (or another) will recapture the prey and commence boring a new borehole, elsewhere on the prey shell. Sometimes the new hole will coincidentally overlap the older hole; but studies have shown that naticids cannot recognize their own previous borehole and resume drilling there (thereby saving considerable time) (Kitchell et al., 1981: 539). The related problem of multiple complete boreholes again suggests interruption of prédation after the completion of a borehole. Obviously there is an evolutionary disadvantage in not recognizing previous boreholes (complete or incomplete); the stereotypy of naticid predatory patterns may not be sufficiently flexible (Vermeij, 1982: 707; Kitchell et a!., 1986).

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In an analysis of the Miocene Strioterebrum monidum from the Caribbean, Kitchell et a!. (1986: 294-5) found extremely large numbers of shells with multiple boreholes; one such had 15, of which 12 were incomplete and three had penetrated the prey shell but were not sufficiently wide to allow passage of the proboscis. Further studies on living terebrids by these authors confirmed that some species of this prey family are highly agile and can repeatedly escape naticid prédation during the boring actions. Earlier, Vermeij et al. (1980: table 2) showed rather high rates (to 40%) of incomplete boreholes in various Recent terebrids; G. J. Vermeij (in litt.) suggested that the pungent odor of terebrids and olivids may represent a chemical defense against prédation.

Fischer (1962b: 97) found that in a large sample (n = 1,126) of the Eocene turritellid Mesalia, 70.9% had naticid boreholes. Of the bored specimens, 84.8% had a single complete borehole (of which a tenth also had one to several incomplete boreholes); 4.2% had multiple complete boreholes; 8.7% had a single incomplete borehole; and 2.3% had multiple incomplete boreholes. Kitchell et al.

(1981: 542) observed that the lucinid Pseudomiltfia floridana had a ratio of incomplete to complete boreholes of 0.54:1. This taxon was stated to be polymorphic for shell thickness; the thicker shells were more likely to have incomplete boreholes.

An important recent discovery was that some bivalve prey, primarily in the tropics, are preferentially bored through the edge of the valves (Taylor, 1980: 175; Vermeij, 1980: 330); not only is the shell thinner there, but also the prey shell is unsculptured and easier to bore (Ansell & Morton, 1985). The latter authors found that some species (i.e. of Polinices) regularly edge-bored Bassina, while Glossaulax did not; that genus may preferentially bore other prey taxa. Some elements of "learning" (conditioning) may be involved in these responses to shell sculpture.

The razor clams {Ensis, Solen) have been shown to be typically consumed by naticids without boring, because when the valves are

contracted, there are still sizable pedal and siphonal gapes through which the naticid proboscis can be inserted (Turner, 1955; Edwards, 1975; Schneider, 1981; Frey et al., 1987); this was also shown for Tresus (Reid & Fiesen, 1980: 32). Edwards & Huebner (1977) noted that Mya was not consumed directly through its large siphonal gape; instead, naticids always bored through the valve; possibly the siphonal tissue deters feeding activities. Eartier, Agersborg (1920: 421) had claimed that Mya and various other clams could be suffocated and directly consumed by Euspira lewisii; this now seems doubtful. Vermeij & Veil (1978) found that the frequency of gaping bivalves in marine faunas decreased from the Arctic to the tropics and noted that this was correlated with the increase in shell boring and other prédation sources in warmer habitats.

Some gastropod prey can be attacked through the aperture, as the corneous operculum is flexible enough for the proboscis to be inserted around the margins (Hughes, 1985). Edwards (1969: 327) found that some Olivella prey were consumed without boring, and suggested that either the naticid could force the operculum, or else the prey "suffocates while wrapped in the predator's foot and relaxes," allowing the predator direct access to prey tissues. Interestingly, Yochelson et al.

(1983: 11) speculated that the stereotypy of naticid boring precluded their attacking scaphopods directly through the open apertural end; but they suggested that it was more likely that once the scaphopod had retracted posteriorly, the naticid proboscis would not be able to reach the prey tissues.

As mentioned earlier, the tropical Indo-Pacific Polinices mammilla is able to "suffocate" and consume bivalve prey without boring. Ansell & Morton (1987) documented that this non-boring prédation, in aquarium experiments, accounted for 14% to 54% of the bivalve mortality (according to prey species). This example, and those in the preceding two paragraphs, would greatly complicate community analyses (especially of fossils!) since no "traces" of naticid prédation would be left on the post-mortem prey shell.

It should be noted that the results of several studies of naticid prédation were misinterpreted as concluding that a significant number of the prey were consumed without boring (Kitchell et al., 1986: 297). Thus, Edwards (1975: 17) found that about 75% of the prey were bored and the remainder died of other

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causes; Taylor et al. (1980: 397) erroneously took this to mean that the latter 25°o of the prey were consumed (by naticids) without being bored. Similarly, Medcof & Thurber (1 958) misinterpreted their own data to assume that all the empty, non-bored bivalve prey shells were consumed by naticid predators without bohng; this overlooked other mortality sources. Another study (Bernard, 1967) stated that 'in limited aquarium observation, over 60% of Saxidomus consumed showed no drill marks" (p. 9); and, again, ". . . in aquaria tests 25% of clams [Saxidomus giganteus] consumed by Polinices [= Euspira] lewisi bore no marks at all" (p. 10); the discrepancy in numbers is irreconcilable and all bivalve mortality was erroneously attributed to naticid prédation.

D. Prey Defense Mechanisms

Ansell (1969) and Carter (1968) provided a general overview of defense mechanisms in various marine mollusks. Many bivalves show leaping or rapid burrowing in response to contact by naticids. Laws & Laws (1972; fig. 1) described the escape response of the Australian Donacilla angusta. which leaps or pops out onto the surface, thereby evading the burrowing naticid predator; similar responses were shown for Ensis directus (Turner, 1955; Schneider, 1982) and Ruditapes ptiilippinarum (Rodrigues, 1986). Either rapid or deep burrowing (or both), can serve as an escape mechanism (Vermeij, 1983a) for bivalve prey.

Ansell & Morton (1985; 656) found that the anomalodesmatan bivalves Lyonsia and Pandora seemed to escape naticid prédation "by coating the postenor edge of the shell with mucus to which sand grains adhere"; presumably this somehow deterred naticid prédation.

Corbulid bivalves have been the object of several paleoecological studies; corbulids are noteworthy for their well-developed conchiolin layer (within the valve) which serves as a fairly effective deterrent to gastropod prédation (Lewy & Samtleben, 1979). Furthermore, most successful boreholes are in the right valve, since there is well-developed periostracum on the left valve of corbulids which also deters predators. Complete boreholes in corbulid valves have a special form, with a considerably narrowed inner margin below the conchiolin layer (De Cauwer, 1985; figs. 1d, le). Kelley (1989a: 446-7) also found considerably reduced successful prédation on Corbula and suggested that the low level of selectivity of prey size and borehole siting may also account for the high rate of unsuccessful prédation (60% of boreholes nonfunctional). Lewy & Samtleben (1979: 350) suggested that the conchiolin layer serves as a compensation for the slow mobility and shallow burrowing of corbulids.

Alternative "defense" strategies of two bivalves were discussed by Commito (1982): Mya arenaria grows rapidly to a large size (and deferring reproduction until then), thereby escaping naticid prédation [= size refuge], whereas Macoma balthica instead grows slowly, reproduces early, and escapes most naticid prédation by deep burrowing [=

spatial refuge]. Of course, Mya is subject to naticid prédation while it is still small. The former mechanism was used by Hutchings & Haedrich (1984) to explain the size structure of deep-water nuculanids subject to naticid and fish prédation. Actually, these "alternative" life history patterns may represent phylogenetic constraints rather than direct adaptations to naticid prédation, per se.

Ansell & Morton (1985) discovered that removal of the sculptural lamellae on the shells of the venerid Bassina led to increased boring prédation through the shell sides. Otherwise the naticids bored through the valve edges which do not have sculpture. This experimental observation demonstrated the function of sculpture as a prey shell defense mechanism in addition to stabilizing the bivalve in soft sediments.

Bayliss (1986) found that among bivalve prey, the species with the thinnest shell was preferentially preyed upon by naticids. Hingston (1985: table 4) noted that increased prey shell sculpture led to increased frequency of unsuccessful (incomplete) boreholes. Dudley & Vermeij (1978; 439) concluded that strong spiral ribs usually deterred boring in turritellids. Kelley (1982a; 46) reported that uncrenulated (male) shells of Astarte were more likely to be bored than were crenulated (female) shells; however this genus is protandrous, and the resulting size differences (between sexes) may be sufficient to explain differences in prédation rate (given that the smaller males are less likely to escape prédation).

Boggs et al. (1984), using Mercenaria mercenaria prey, artificially ground-down the shell surface to half the normal thickness, and tested the effects on prédation by Neverita duplicata. They found that naticids could not

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learn to differentiate between normal and thin-shelled prey, although the latter took considerably less time to bore. The same results were found by Rodrigues et al. (1987) for Neverita didyma preying on Ruditapes ptiilippinarum. In some respects, these studies are of questionable value since it has not been shown that gastropods have any sensory mechanism for "determining" shell thickness (or shell weight). It is true that preying on thinner prey freed up additional time for foraging; surely the snails are incapable of this realization because they have no method for recognizing the thinner prey. This is an interesting case of a hypothetical coevolutionary response that does not initiate an "arms race."

E. Food Webs, Energy Flow and Physiological Efficiencies

Food webs are attempts to diagram the overall trophic structure of an ecological community (predators, herbivores, primary producers, detritivores). Elucidation of the structure of a food web and the strength (or quantity of interactions) of each link (chain) facilitates analyses of community energy flow and population dynamics. As infaunal predators, naticids (with other infaunal polychaetes, crustaceans, and nemerteans) represent an often overlooked level of prédation, in addition to the more conspicuous epibenthic predators (asteroids, fish and crabs) (Commito & Ambrose, 1985). An example of the complexity involved is that both asteroids and naticids prey on bivalves, whereas some asteroids also prey on naticids (Christenson, 1970: 67); the same multiple interactions also occur with respect to crabs and fishes. Relatively little research has been done on determining the complete food webs for soft-bottom communities, in contrast to better-known rocky intertidal communities; this reflects the ease of access and analysis of the latter fauna.

Several paleocological studies have attempted to elucidate community structure and food webs, based primarily on an analysis of shell boring and breaking prédation (Hoffman & Szubzda, 1976; Stanton & Nelson, 1980; Stanton et al., 1981; Stump, 1975; Taylor et al., 1983). While of great heuristic value in facilitating comparisons between fossil communities (as well as with Recent communities), these studies are limited by the indeterminate nature of mortality that leaves no "traces," as well as shell-removing agents, the latter skewing the results towards the remaining predatory agents.

It is important to realize that naticid prédation represents only a part of the sum of all prédation in soft-bottom communities; several authors have carefully reviewed the diversity and importance of other predators in these habitats (Cadée, 1968; Carter, 1968; Vermeij, 1978). Thus, Green (1969) found that naticids accounted for 9% of the mortality of the tropical bivalve Notospisula parva; shell-crushing skates were responsible for over 60% of the mortality; the remainder was due to other factors (disease or abiotic agents). The latter, non-predatory sources of mortality are just as important but virtually impossible to determine precisely from fossil or beach assemblages (i.e., an empty, undamaged shell may be the outcome of parasitism, other disease, sedimentation, or other agents) (Hoffman, 1976a).

A series of excellent physiological studies was conducted by Ansell and Macé on the European Euspira alderi. Distinct periods of shell growth were followed by egg collar production; feeding was considerably greater during the latter stage, since over 90% of non-respired assimilated energy is used for reproduction (Ansell & Macé, 1978; Ansell, 1982a-b). Prédation rates increased with temperature (Macé, 1981a); and oxygen consumption rates (= respiration) were affected by the prey type and quantity (Macé, 1981b; Macé & Ansell, 1982). Each week, an adult naticid consumed up to its own (dry) weight in prey tissue [Tellina tenius] (Ansell, 1982a); this is limited by the extensive time spent in obtaining suitable prey. Macé (1981c) found that energy assimilation efficiency is about 60% during reproductive periods, and only 40% at other times. About 50-60% of the consumed energy is, however, "lost": not accounted for by growth, respiration (maintenance) or reproduction. Ansell (1982b) suggested that some of this may be accounted for by the mucus that is essential for prey capture and predator avoidance; much of the remainder is represented by feces and unconsumed prey tissue, but Berry (1983) was unable to calculate the energetic costs or losses due to mucus or feces. Bayliss (1986), using the same naticid species, found that about 24% of the time was spent drilling, 11%-18% ingesting prey tissue, and the remaining time in other activities, typically quiescent.

Related physiological studies on the temperate Neverita duplicata (in Massachusetts)

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showed that the feeding season was only about 35 weeks, during which approximately 1 .85 prey [Mya arenaria) were consumed per week. The naticids consumed about 1% of their body weight in prey on a daily basis, and the overall growth efficiency rates (snail growth in kilojoules per clam tissue consumed in kilojoules) declined from almost 50% in young snails to 16% in older snails (Edwards & Huebner, 1977; Huebner & Edwards, 1981).

Another factor of importance in calculating energy budgets is whether or not all the prey tissue is consumed. Thus, for a high-spired gastropod prey, some of the apical tissues may not be reached by the proboscis. Edwards & Huebner (1977) found that when feeding on Mya. only about 80% of the prey tissues were consumed (i.e. the "energy rich, low-ash content tissues"); proboscoidal access is not at issue here and this may reflect the less-palatable nature of the mantle edge and siphonal tissues of Mya.

Broom (1982) determined the "consumption rate" equation of feeding efficiency: this represents the mg dry weight of prey consumed per day, as a function of predator body (wet) weight. Thus, for Natica maculosa feeding on Anadara granosa, the allometric equation was CW = 9.13 (W)' °°^^ where W = predator wet weight (in grams). Similarly, Gnffiths (1981) found that the consumption rates (of bivalve prey, Choromytilus menodionalis) Increased 4.5 fold over a 55% increase in predator (Natica tecta) size.

Many of these studies were based on laboratory (aquaria) observations. These, of course, are a simplification or modification of reality (field behavior). Bayliss (1986: 46) cogently noted that "the artificial and enclosed environment in an aquarium increases the predator's ability to detect and capture a prey item as well as reducing the prey's ability to avoid and escape from the predator. " Also, intertidal naticids are usually quiescent dunng low tide; in aquaria where they are continually submerged, the duration of activity is more extensive. Many laboratory studies (e.g. Rodrigues, 1986) used an aquanum sand depth barely greater than the prey or predator size; this does not allow for normal burrowing patterns. Kitchen et al. (1986: 297) noted that in their aquaria, the prey frequently "die, gape and decompose without the predator taking any part in the process"; this suggests that their prey were usually moribund or otherwise unhealthy, and leads one to question the validity of prédation studies on these weakened prey. These caveats should be considered when calculating feeding rates, energy budgets, and related trophic measurements based on laboratory studies.

A typical example of the effects of naticid prédation on prey population dynamics is that of Ansell (1960) who found that of first-year Venus [- Chamelea] stnatula. 40% of the total mortality [= 15% of all individuals] was due to naticids; for the second-year cohort, only 15% of all mortality [= 5% of the cohort] was naticid prédation; and for the third-year cohort [the last], only about 1% of all mortality was due to naticids. Clearly, prédation by Euspira alderi affects primarily the younger cohorts; disease or other predators affect the older cohorts.

.Another interesting taphonomic-ecological phenomenon is that of 'ti)each sorting" or the differential post-mortem "survival" of valves of different bivalves (interspecific and intraspecific analyses), comparing both right vs. left valves and bored vs. unbored valves (Lever et al., 1961; Lever & Thijssen, 1968; Martineil & De Porta, 1980). The critical question is whether or not bored valves are differentially susceptible to post-mortem damage which would affect their representation in the fossil (or "beach shell ") assemblage (Dudley & Vermeij, 1978: 437). One must also determine the extent of other shell-breaking prédation that wholly removes the shells from the assemblage.

The studies of Lever and colleagues found that valves with boreholes (natural or artificial) traveled shorter distances but were more likely to end up higher on the shore (than non-bored valves), because of the biomechanics of fluid flow through and around bored valves. Thus, the "hole effect" is the upward transport of bored valves. The differential transport of right and left valves may also occur, resulting in greatly distorted ratios thereof in a beach assemblage. Indeed, it is possible that some paleontological studies showing "differences" in boring rates between valves may actually be a consequence of this differential sorting. A problem with such studies is that the hydrodynamic properties of bivalve shells can vary between taxa, and the biomechanical effects of one shell morphology may well be the opposite of those of a different morphology.

F. Enemies and Control of Naticids

Asteroids (starfishes or seastars) are important predators of naticids (Agersborg,

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1920; Christenson, 1970); some naticid prey will ward off the asteroid by extension of the foot over the shell followed by mucus secretion (Ansell, 1969; Margolin, 1975). The latter author documented that Natica stercusmuscarum could respond to Astropecten by rasping off the spines and consuming the tube feet, deterhng the starfish. Clarke (1956) noted that Nassarius trivittatus feeds upon the egg collars of Euspira heros, serving as a means of control. Ironically, this nassariid is, in turn, preyed upon by adult naticids!

Frequently, naticids are "blamed" for observed declines in populations of commercial shellfish (soft shell clams, quahogs, etc.), and oyster beds may be disrupted as naticids burrow through them in search of other prey items (Agersborg, 1920: 420). Because oysters are now more commonly cultivated on stakes or lines off the substrate, this may now be less of a problem. Edwards & Huebner (1977: 1231) cogently noted that "bored shells . . . are thus an exaggerated indicator of [naticid] mortality . . ." because other predators (arthropods, fish, birds, humans) remove or otherwise destroy bivalve shells. These authors further stated that naticid predators are an easy scapegoat to take the blame for ". . . human exploitation patterns, a sensitive issue." The various mechanisms and their success (or lack thereof) for the control of "pests" of shellfish were reviewed by Korringa (1952: 347-351); hand collecting is particularly ineffective (Turner et al., 1948; Medcof & Thurber, 1958). Carhker (1981: 417) suggested that ecological control, involving species-specific pheromones or deterrents, might be successful. There remains the often unacknowledged dilemma that not only is it impractical (or even impossible) to eliminate these predators, but also the resulting impact on the overall community structure and food web may actually be more deleterious than the effects of the predators themselves on the shellfish.

G. Macroevolutionary Patterns and Evolutionary Escalation

If, as claimed by Fürsich & Jablonski (1984), the Triassic boreholes are attributable to naticids, then the parallel evolution of the naticid boring habit twice (Thassic and Cretaceous) undoubtedly reflected the canalization or phylogenetic constraints of shell-boring: there are only so many ways a shell can be bored, and the underlying mechanisms may

have remained quiescent in the Naticidae during the Jurassic. However, it remains unclear whether the Triassic predators are indeed naticids, or how the Jurassic naticids may have fed (possibly as scavengers).

Taylor et al. (1980: fig. 16) presented a hypothetical scenario of the evolutionary radiation of gastropod prédation. Generalized proboscis probing was subsequently supplemented by pedal manipulation, which led variously to shell boring, wedging, chipping, or pedal suffocation. It can be assumed that these initial stages represented preadaptations to shell boring; however, the specific origins of the complex accessory boring organ remain uncertain. The independent evolution of shell boring in a number of molluscan taxa represents convergent evolution; the structures and processes are not necessarily homologous. (See "Diversity of Boring Prédation" above for further comparisons).

The Cretaceous radiation of naticids is part of the Mesozoic marine revolution, involving the increase in diversity of many modern marine predators as a consequence of the "increase in shelled food supply resulting from the occupation of new adaptive zones by infaunal bivalves and by shell-inhabiting hermit crabs" (Vermeij, 1977: 245). Specifically, the shift of bivalves from predominantely epifaunal and byssate forms to infaunal, siphonate forms served as an escape from the then-dominant epifaunal and pelagic predators [cephalopods, asteroids, sharks and marine reptiles] (see also Taylor, 1 981 : 236) and subsequently led to selection favoring infaunal predators. If the early Mesozoic naticids were not burrowers (as suggested by their shell morphology), then burrowing in combination with shell boring would have opened up a new adaptive zone for the Cretaceous naticids. At the same time, the diversification of other sandy-habitat gastropods (especially turhtellids, turrids and terebrids) provided further infaunal prey for naticids (Taylor et al., 1980: 399).

An important biogeographical phenomenon is the pattern of latitudinal diversity (pole-equator) of predatory prosobranch gastropods. For most of these marine families, including the Naticidae, there is a strong increase in species diversity from the poles to the tropical regions (the two exceptions are the Buccinidae and Turhdae) (Taylor & Taylor, 1977; Taylor et al., 1980: 381-3). Correlated with this gradient, Dudley & Vermeij (1978: 439) showed a marked equatorward

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increase in boring prédation in Turritella. Subsequently Vermeij et al. (1989), for bivalve prey, actually observed an equatorward decrease in the frequency of complete boreholes (and a correlated equatorward increase in the frequency of incomplete boreholes): they suggested that the turntellids were an unexplained exception to this more general pattern.

It appears that since the Cretaceous, the general mechanisms and consequences of naticid prédation have not greatly changed. To be sure, the prey sources have changed, not only due to origination and extinction of prey taxa, but also because of changes in prey defense mechanisms. However, the overall "strategy" of naticid prédation has persisted for the last 100 million years (Kitchell, 1 987). It is possible that the naticids, following their late Cretaceous-early Tertiary adaptive radiation, have now reached their maximum taxonomic diversity (e.g. Sohl, 1969: fig. 1) and are at stasis which may lead to eventual decline in the absence of evolutionary innovations facilitating further expansion. The highly stereotyped nature of naticid prédation suggests that their canalization may be so great as to preclude further breakthroughs (but consider the non-boring, suffocation prédation of Polinices mammilla).

With the rise of muricids in the later Tertiary, the naticids may have shifted from gastropod to bivalve prey, as suggested by Adegoke & Tevesz (1974). Hoffman et al. (1974) noted that in a Miocene assemblage, naticid boreholes were found mostly in smooth prey whereas muricid boreholes were primarily in ribbed (sculptured) prey: however the former prey are more likely to be infaunal than the latter, which may affect these results. Within the Maryland Miocene. Kelley (1982a) found that naticid prédation shifted from predominantly bivalve prey in the Calvert and Choptank formations to gastropod prey in the St. Marys Formation, correlated with the increase in diversity of prey gastropods in the latter formation. Kelley's results may be a preservational artifact, as the St. Mary's has a much better representation of gastropods than do the earlier formations (G. J. Vermeij, in litt.). Clearly, one also needs to account for changes in the relative abundances of infaunal prey sources; trends as suggested by Adegoke & Tevesz (1974) may not be applicable on a global scale. In addition, the study of naticids has been primarily in a few restricted habitats: more comprehensive analyses of tropical sub-littoral communities may show other naticid prédation patterns.

Kelley (1982a) suggested that extensive naticid and other prédation on bivalves increased prey species diversity, perhaps by reducing competitive interactions. Although ecologists recognize several factors that affect species diversity, prédation is undoubtedly one of the more important, and one that can be easily recognized in the fossil record. Perturbation experiments involving predator-exclusion cages were used by Wiltse (1980b) to analyze the role of the western Atlantic Neventa duplicata in its community structure: she found that snail prédation and disturbance (due to burrowing) actually decreased the community species diversity by eliminating the rare species and blocking strong competitive interactions.

Kitchell and colleagues (Kitchell et al., 1 981 : Kitchell, 1982, 1983, 1986: DeAngelis et al., 1 984, 1 985, 1 989) expanded upon their model of the energetics of naticid prédation to develop models of coevolution of naticids and their prey. Coevolution, or the reciprocal evolutionary interactions of two taxa, is an important, albeit difficult to quantify, aspect of evolutionary biology. There has been considerable disagreement as to how tightly or broadly coevolution should be defined or restricted. Indeed, almost any evolutionary trend can be "explained" as part of a coevolutionary process (Vermeij, 1982: 711-2). Instead of recognizing coevolution as "all evolution resulting from biological interactions," it is much more useful to restrict it to "reciprocal adaptation involving the heritable traits of two or more species" (Vermeij, 1983b: 311). These models of naticid-prey coevolution are subject to the same caveats mentioned earlier under the discussion of the previous models. Nevertheless, I shall attempt to summarize their scenarios.

First, one can hypothesize that some sorts of evolutionary "arms races" are involved, with the prey evolving various antipredatory adaptations, but with the predator also evolving new or changed features. One consequence is that "multiple adaptive tactics produce multiple directionality" (Kitchell et al., 1981 : 550), meaning that diversity may result as different prey follow alternative strategies and the same is true for different predators. This may result in character displacement or other isolating mechanisms resulting in speciation (Kitchell, 1983).

A direct test of these coevolutionary processes, at least for naticid predators, was conducted by Kitchell (1982) who analyzed Marincovich's stratigraphie data for the eastern Pacific Neogene naticid fauna and concluded

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that predator "efficiency" increased over geological time. Specifically, size, globosity and streamlining of the shell all increased, as did the proportion of apertural area to shell area and the general diversification of morphology (the latter not fully explained). In some respects these are all a consequence of general phyletic size increase, and may not be directly due to coevolution.

Further refinements of their coevolutionary models predicted that in the absence of predators, prey will reproduce early (i.e., at small sizes); whereas in the presence of predators, prey will show delayed reproduction at larger sizes (DeAngelis et al., 1984). More complex age-structured models tested the prey energy-allocation functions (growth vs. reproduction) as a consequence of prédation levels, and resulted in three alternative ecological strategies for bivalve prey as coevolutionary responses: delayed reproduction to large size, early reproduction, or increased shell thickness. Needless to say, the numerous assumptions (DeAngelis et al., 1985: 836) severely constrain the value of their coevolutionary model. In particular, they assume that no other factors affect the population dynamics of the naticids or their prey; this overlooks other predators, disease and parasitism, and abiotic mortality sources, all of which (together and severally) are often of greater importance to the prey than are naticids, as has been documented in the other studies discussed herein. Of course, with respect to the evolution of shell morphology, the latter factors are not easily measured or of great significance. The results of their models largely corroborated the conclusions of previous ecological studies.

Edge-boring of bivalve prey represents an escalation in the evolutionary "arms race" as an adaptive response to the presence of prey sculptural elements and shell-thickening. Similarly, non-boring prédation (suffocation) also represents an alternative strategy (Ansell & Morton, 1987: 117); the selective advantages presumably entail a reduction in the energetic costs of boring. Further study should reveal whether some prey taxa are resistant to these novel prédation mechanisms. The phylogenetic correlations of these two traits remain uncertain; at the present time, they are only known for a few species from the tropical Indo-Pacific.

To briefly summarize these ecological studies: (a) There is a general positive correlation between predator and prey size; size selectivity is shown as larger prey often have a size refuge from prédation, (b) Prey defense mechanisms not only help prevent prey capture, but also may lead to interruptions of prédation as shown by incomplete boreholes in the prey shell, (c) The successful mode of naticid prédation is limited by its seeming stereotypy (inflexibility), (d) The intriguing possibilities of predator-prey coevolution (arms races) remain unproven for specific cases.

FUTURE DIRECTIONS

This review has suggested several areas needing further research. They are tabulated below; readers will undoubtedly recognize yet other problems amenable to future studies.

The detection of prey by naticids remains a puzzle: elucidation of the potential interactions of chemosensory mechanisms (osphradium) vs. echolocation (Kitching & Pearson, 1 981). A related mechanistic problem is to determine the precise biochemical constituents of the accessory boring organ secretion in naticids and the mode of function of shell dissolution.

More ecologically oriented approaches could include sophisticated field analyses of prey choice, entailing controlled manipulations and perturbation experiments (remove one species at a time). Further quantification of the various links of soft-bottom community food webs to determine more precisely the quantitative role of naticids in this habitat. Development of methods of ecological control of naticid predators of shellfish.

Paleontologists could analyze Paleoceno faunas for gastropod boring prédation; and conduct more detailed studies of Jurassic and Early Cretaceous faunas to supply information on changes in prédation and shell form during that time (Vermeij, 1987: 238-9). Further study of the phylogenetic position of the Thassic shell borers and the earty fossil record of naticids to unravel the complexities of the origin(s) of shell boring of the naticid type.

Study of boring prédation from the cold temperature southern oceans and the sub-Antarctic would be most desirable. The presence of several phylogenetically primitive nat-

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¡cid taxa in those faunas would provide further clues as to the relationships between naticid phylogeny and boring prédation. It remains uncertain whether the most primitive subfamily, the Ampullospirinae [Tnassic? — Recent] are shell borers.

Further research on the geographical and phylogenetic extent of epifaunal prédation, non-boring suffocation, and edge-boring would also add to our knowledge of the phylogenetic correlations of prédation mechanisms.

CONCLUSIONS

(A) Bored or punched holes in prey shells are made by nine taxa of manne predators: naticid, muncid & capulid snails, octopods, Pseudostylochus (Turbellaria) and Asemichthys (Pisces), all in mollusk shells; cassid snails in echinoids; Okadaia (Nudibranchia) in calcareous polychaete tubes; and nematodes in foraminiferal tests. Some terrestnal zonitid snails are also shell-borers. Shell-crushing predators (sharks, crustaceans) sometimes leave holes in othenA/ise intact prey shells.

(B) Following prey capture, naticid boring is accomplished by alternate application to the prey shell of the radula and the proboscoideal secretory accessory boring organ. The distinctive naticid borehole is countersunk, with beveled edges.

(C) The data on naticid prey show that many soft-bottom families of bivalves and gastropods are subject to naticid prédation. Rocky-habitat taxa escape the infaunal naticids.

(D) Boring prédation potentially attributable to naticids originated in the Triassic but shortly became extinct. The naticid boring habit definitively evolved in the Late Cretaceous and has been documented through Holocene faunas, with an unstudied gap in the Paleoceno. No clear trends in rates of boring prédation since the Cretaceous are obvious.

(E) Most studies have shown a positive correlation between predator size and prey size; also, smaller prey are usually subject to higher rates of naticid prédation. Incomplete boreholes reflect interruptions of prédation; multiple boreholes demonstrate inflexible stereotypy of naticid boring. Prey defense can take several forms; leaping or burrowing; thick or sculptured shells; chemical defenses; growth to large size; and the corbulid conchiolin layer. Non-boring prédation, either through gaping shells or pedal suffocation, greatly confounds ecological studies since no signs of prédation are left on the prey shell.

(F) Naticid prédation is an important and easily documented link in the food web of marine soft-bottom communities; other predators often crush or remove their prey without leaving recognizable remains.

(G) The evolution of naticid boring prédation is part of the Mesozoic marine revolution entailing the diversification of infaunal bivalves and other gastropods which greatly increased naticid prey sources. Evolutionary escalation (defenses) on the part of prey taxa may have occurred since the Cretaceous; attempts to prove specific coevolutionary trends have been unsuccessful.

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APPENDIX

An * indicates that no species was given; "spp." indicates that more than two species of that genus were reported on in one reference. I have not included the taxa reported on by

Arua (1989) or Arua & Hoque (1989a-c) due to the questionable nature of their borehole determinations.

A. Class Gastropoda. Subclass Prosobranchia.

Order Archaeogastropoda. Trochoidea. Trochidae:

Calliostoma laugiein [Vignali & Galleni, 1987]

Gibbula vana [Vignali & Galleni, 1987]

Helicocryptus radiatus [Taylor et al., 1983]

Jujubinus exasperatus [Vignali & Galleni, 1987]

Margantes monolifera [Taylor et al., 1983]

Monilea' [Kohn, unpub.]

Umbonium vestianum [Berry, 1982]

Cyclostrematidae:

Pseudoliotina' [Taylor et al., 1983]

Turbinidae:

Turbo' [Kohn, unpub]

Neritoidea. Neritidae:

Nenta funiculata [Hughes, 1985]

N. scabricosta [Hughes, 1985]

Neritina virgínea [Jackson, 1972]

Theodoxus luteofasciatus [Stump, 1975]

Order Mesogastropoda. Littorinoidea. Littorinidae:

Littonna littorea [Edwards, 1975]

Rissoidea. Hydrobiidae:

Hydrobia andrussowi [Kojumdjieva, 1974]

Rissoidae:

Alvania alexandrae [Hoffman et al., 1974]

Ihungia ponden [Maxwell, 1988)

Mohrensternia angulata [Kojumdjieva, 1974]

M. inflata [Kojumdjieva, 1974]

Rissoa inconspicua [Fretter & Manly, 1979]

Rissoina podolica [Hoffman et al., 1974]

[Begin Page: Page 189]

Caecidae:

Caecum glabrum [Hoffman et al.

Vitrinellidae:

Circulus* [Hoffman et al., 1974]

1974]

Cerithioidea. Cerithiidae:

Argyropeza' [Kohn, unpub.]

Bittium' [Berg, 1976; Taylor, 1970]

a reticulatum [Hoffman et al., 1974]

Cerithium europeum [Kojumdjieva, 1974]

C. vahabile [Jackson, 1972]

C. vulgatum [Vignali & Galleni, 1987]

Rhinoclavis* [Kohn, unpub.]

Procerithiidae:

Cirsocerithium gracile [Taylor et al., 1983]

Diastomatidae:

Sandbergeria perpusilla [Hoffman et al., 1974]

Fossariidae:

"Fossarus" granosus [Taylor et al., 1983]

Turritellidae;

Archimediella spirata [Robba & Ostinelli, 1975]

Mesalia spp. [Fischer, 1962]

M. amekiensis [Adegoke & Tevesz, 1974]

M. regularis [Taylor, 1 970]

Turritella spp. [Dudley & Vermeij, 1978]

T. badensis [Kojumdjieva, 1974]

T. b/en/asz/ [Kojumdjieva, 1974]

T. granulata [Taylor et al., 1983]

7". subangulata [Kojumdjieva, 1974]

T. tricarinata [Hoffman & Martinell, 1984]

Stromboidea. Aporrhaidae:

Aporrhais pespelecani [MartineW & Marquina, 1980]

A. uttingerianus [Martinell & Marquina, 1980]

Drepanocheilus calcarata [Taylor et al., 1983]

D. neglecta [Taylor et al., 1983]

Strombidae:

Rimella fissurella [Taylor, 1 970]

Strombus* [Kohn, unpub.]

Tibia unidigitata [Adegoke & Tevesz, 1974]

Hipponicoidea. Hipponicidae:

HIpponix' [Kohn, unpub.]

Vanikoriidae:

'Vanil<oropsis" CÍ. albus [Taylor et al., 1983]

Tonnoidea. Cassidae:

Semicassis wannoensis [Hingston, 1985]

Cymatiidae:

Cymatium' [Kohn, unpub.]

Suborder Heteroglossa. Cerithiopsioidea. Cerithiopsidae:

Cerithiopsis tubercularis [Hoffman et al., 1974]

Triphoroidea. Triphohdae:

Triphora perversa [Hoffman et al., 1974]

Epitonioidea. Epitoniidae:

Confusiscala fittoni [Taylor et al., 1983]

Epitonium spinosa [Hoffman et al., 1974]

Eulimoidea. Eulimidae;

Eulima subulata [Hoffman et al., 1974]

Strombiformis glaber [V\gr\a\'\ & Galleni, 1987]

Rissoelloidea. Rissoellidae:

Rissoella* [Berg, 1976]

Order Neogastropoda. Muricoidea. Muhcidae;

Blackdownea quadrata [Taylor et al., 1983]

Eupleura caudata [Flower, 1954]

Hadrlania craticulata [Martinell & Marquina, 1980]

Hexaplex benedeica [Adegoke & Tevesz, 1974]

Morula' [Kohn, unpub.]

Nassa restitutiana [Kojumdjieva, 1974]

N. dujardini [Hoffman et al., 1974]

Paramorea lineata [Taylor et a!., 1983]

Pterynotus' [Adegoke & Tevesz, 1974]

Terefundus lamelliferus [Maxwell, 1988]

L/rosa/p/nx [Flower, 1954]

Buccinidae:

Cantharus' [Kohn, unpub.]

Phos* [Kohn, unpub.]

Siphonalia* [Kohn, unpub.]

Columbellidae:

Mitrella' [Adegoke & Tevesz, 1974]

M. m/nor [Hoffman & Martinell, 1984]

M. nassoides [Kojumdjieva, 1974]

Nassariidae:

Amyclina spp. [Robba & Ostinelli, 1975]

Cyllene' [Adegoke & Tevesz, 1974]

Dorsanum duplicatum [Kojumdjieva, 1974]

Nassarius elatus [Hoffman & Martinell, 1984]

N. italicus [Martinell & Marquina, 1980]

N. obsoletus [Edwards, 1975]

N. perpinguis [Berg & Nishenko, 1975]

N. pygmaeus [Hoffman & Martinell, 1984]

N. semistriatus [Hoffman & Martinell, 1984]

N. tiarula [Stump, 1 795]

N. trivittatus [Edwards, 1975]

Niotha crassigranosa [Hingston, 1985]

Plicarcularia leptospira [Broom, 1983]

Fasciolariidae:

Colubraria' [Kohn, unpub.]

Falslcolus tangituensis [Maxwell, 1988]

Fusinus* [Kohn, unpub.]

Granulifusus' [Kohn, unpub.]

Iscafusus rigidus [Taylor et al., 1983]

Latirus moorei [Stanton et al., 1981]

Peristernia' [Kohn, unpub.]

Turbinellidae [= Vasidae]:

Exilia tve//man/ [Maxwell, 1988]

Olividae:

Alocospira papillata [Hingston, 1985]

Ancilla buccinoides [Taylor, 1 970]

Olivella biplicata [Edwards, 1969]

Marginellidae:

Marginella spp. [Taylor, 1970]

Protoglnella bembix [Maxwell, 1988]

Mitridae:

Cancilla' [Kohn, unpub.]

Mitra Orientalis [Kojumdjieva, 1974]

Scabricola' [Kohn, unpub.]

Subcancilla* [Kohn, unpub.]

Volutomitridae:

Microvoluta nodulata [Maxwell, 1988]

[Begin Page: Page 190]

Costellariidae [= Vexlllidae]:

Austromitra' [Hingston, 1985]

Vexillium' [Kohn. unpub.]

Cancellarioidea. Cancellanidae:

Bonellitia amekiensis [Adegoke & Tevesz. 1974]

B. serrata [Martinen & Marquina, 1980]

Inglisella parva [Maxwell. 1988]

/. allophyla [Maxwell, 1988]

Sydaphera wannonensis [Hingston, 1985]

Conoidea. Conldae;

Conus dujardini [Kojumdjieva, 1974]

parisiensis [Taylor, 1970]

Turridae:

Bela brachystoma [Hoffman & Martinell. 1984]

B. vulpécula [Hoffman & Martinell. 1984]

Brachyioma obtusangula [Martinell & Marquina,

1980]

Clavatula' [Adegoke & Tevesz, 1974]

Clavus spp. [Robba & Ostinelli, 1975]

Comitas nana [Maxwell, 1988]

Crassispira' [Kohn, unpub.)

Cythara subcylindrata [Hoffman et al., 1974]

Eopleurotoma spp. [Adegoke & Tevesz, 1974]

Gemmula' [Kohn, unpub.]

Genota ramosa [Kojumdjieva, 1974]

Hesperiturns nodocannatus [Stanton et al., 1981]

Heterocithara marwicki [Maxwell. 1988]

Lophitoma' [Kohn, unpub.]

Mauidnllia occidentalis [Maxwell, 1988]

Michela trabeatoides [Stanton et al., 1981]

Mioawatena personata [Maxwell, 1988]

Paracomitas beui [Maxwell, 1988]

Pleurotoma' [Adegoke & Tevesz, 1974]

Raphitoma hispidula [Hoffman et al., 1974]

Rugobela' [Maxwell, 1988]

Splendnllia i/e/Za/ [Maxwell, 1988]

Tomopleura' [Maxwell. 1988]

Turricula africana [Adegoke & Tevesz, 1974]

T. dimidiata [Martinell & Marquina, 1980]

Viridoturns powelli [Maxwell, 1988]

Terebridae:

Gemmaterebra catenifera [Hingston, 1985]

Strioterebrunn monidum [Kitchell et al., 1986]

S. pliocenicunn [Martinen & Marquina, 1980]

Terebra spp. [Vermeij et al., 1980]

T. dislócala [Kitchell et al., 1986]

Zeacuminia viapollentia [Maxwell, 1988]

Subclass Heterobranchia. Superorder Allogastropoda.

Architectonicoidea. Architectonicidae:

Architectonica bendeica [Adegoke & Tevesz, 1974]

A. olicatum [Taylor, 1970]

Philippia meditteranea [Vignali & Galleni, 1987]

Pyramidelloidea. Pyramidellidae;

Eulimella conulus [Hoffman et al., 1974]

Evelynella doliella [Maxwell, 1988]

Odostomia' [Adegoke & Tevesz, 1974]

G. conoidea [Hoffman & Martinell, 1984]

Pyramidella digitalis [Hoffman et al., 1974]

P. plicosa [Hoffman & Martinell, 1984]

Pyrgulina interstincta [Hoffman et al., 1974]

Tubonilla rufa [Hoffman & Martinell, 1984]

T. zesulcata [Maxwell, 1988]

Waikura elevata [Maxwell, 1988]

Subclass Opisthobranchia. Order Cephalaspidea,

Philinoidea. Acteonidae:

Acteon réussi [Hoffman et al., 1974]

A. semistnatus [Hoffman & Martinell, 1984]

A. tornatilis [Vignali & Galleni, 1987]

Tornatellaea affinis [Taylor et al., 1983]

T. unlsulcata [Taylor et al., 1983]

Ringiculidae:

Avellana incrassata [Taylor, et al., 1983]

Ringicula auriculata [Hoffman et al., 1974]

R. buccinea [Hoffman & Martinell, 1984]

Scaphandridae:

Acteocina lajonkaireana [Kojumdjieva, 1974]

Cylichina melitopolitana [Kojumdjieva, 1974] rubignosum [Kojumdjieva, 1974]

Scaphiander' [Adegoke & Tevesz, 1 974]

Tornatina heraclitica [Hoffman et al., 1974]

T. trunculata [Hoffman et al., 1974]

Hamineidae:

Atys miliaris [Hoffman et al., 1974]

Retusidae:

Retusa kelloggi [Stanton et al., 1981]

R. truncatula [Hoffman & Martinell, 1984].

B. Class Bivalvia. Subclass Protobranchia. Order
Nucuioida.

Nuculoidea. Nuculidae:

Acila conradi [Colbath, 1985]

Ennucula kalimnae [Hingston, 1985]

Nucula antiquata [Taylor et al., 1983]

N. mixta [Taylor, 1970]

N. nucleus [IHoffman & Szubzda, 1976]

N. obtusa [Taylor et al., 1983]

N. túrgida [Wilson, 1988]

Palaeonucula strigilata [Fürsicn & Jablonski, 1984]

Nuculanoidea. Nuculanidae:

f^esosaccella angulata [Taylor et al., 1983]

/W. Iineata [Taylor et al., 1983]

Nuculana' [Adegoke & Tevesz, 1974]

Nuculana spp. [Colbath, 1985]

N. fragilis [Kojumdjieva, 1974]

N. pella [Vignali & Galleni, 1987]

N. pernula [Hutchings & Haedrich, 1984]

Yoldiidae:

Yoldia' [Colbath, 1985]

V. tfiraciaeformis [Hutchings & Haedrich, 1984]

Malletiidae:

l^alletia* [Kohn, unpub.]

Subclass Pteriomorphia. Order Mytiioida.

Mytiloidea. Mytilidae:

Choromytilus meriodionalis [Griffiths, 1981]

Crenella orbicularis [Taylor et al., 1983]

¡Modiolus auriculatus [Vermeij, 1980]

/W. reversa [Taylor et al., 1983]

Mytilus edulis [Edwards, 1 975]

[Begin Page: Page 191]

Order Arcoida. Arcoidea. Arcidae:

Anadara spp. [Kelley, 1989a]

A. elevata [Dudley & Dudley, 1980]

A. granosa [Broom, 1982]

Adevincta [Colbath, 1985]

A. c/z/uw/ [Kojurdjieva, 1974]

A. thisphila [Dudley & Dudley, 1980]

Barbatia irregularis [Taylor, 1 970]

Bathyarca' [Maxwell, 1988]

Noetiidae:

Arcopsis dissimilis [Darragh & Kendrick, 1980]

Pachecoa declivis [Kitchell, 1982]

Cucullaeidae;

Idonearca glabra [Taylor et al., 1983]

Limopsoidea. Limopsidae:

Limopsis chapmani [Darragh & Kendrick, 1980]

L. beaumarisensis [Hingston, 1985]

L. minuta [Kojurndjieva, 1974].

Giycymerididae: ^

Glycymeris spp. [Thomas, 1976]

G. albolineata [Matsukuma, 1977]

G. rta/// [Hingston, 1985]

G. insubrica [Vignali & Galleni, 1987]

G. pulvinata [Taylor, 1 970]

G. vestita [Matsukuma, 1977]

Glycymerita sublaevis [Taylor et al., 1983]

G. umbonata [Taylor et al., 1983]

Ptehoida. Pterioidea. Cassianellidae;

Cassianella ampezzana [Fürsich & Jablonski, 1984]

Order Limoida. Limoidea. Limidae;

Mysidioptera williamsi [Newton, 1983]

Order Ostreoida. Ostreoidea. Gryphaeidae:

Amphidonte obliquata [Taylor et a!., 1983].

Pectinoidea. Pectinidae;

Chlamys radians [Guerrero & Reyment, 1988]

Pectin opercularis [Boekschoten, 1967]

Pseudamussium similis [Smith, 1932].

Subclass Paleoheterodonta. Order Trigonioida.

Trigonioidea. Trigoniidae:

Rutitrigonia eccentrica [Taylor et a!., 1983]

Subclass Heterodonta. Order Veneroida.

Lucinoidea. Lucinidae:

Codakia bella [Vermel], 1980]

C. orbicularis [Jackson, 1972]

Ctena decussata [Vignali & Galleni, 1987]

C. orbiculata [Jackson, 1972]

Divaricella ornata [Kojumdjieva, 1974]

D. divaricata [Vignali & Galleni, 1987]

Epicodakia' [Kohn, unpub.]

Loripes dentatus [Hoffman et al., 1974]

L. lacteus [Vignali & Galleni, 1987]

Lucina anodonta [Kelley, 1989a]

L. approximata [Stump, 1975]

L. spinifera [Kojumdjieva, 1974]

Lucinella divaricata [Hoffman & Martinell, 1984]

Myrtea papatikiensis [Maxwell, 1988]

Parvilucina costata [Jackson, 1972]

Pseudomiltha floridana [Kitchell et al., 1981]

Wallucina* [Vermeij, 1980]

Fimbriidae:

Mutiella canaliculata [Taylor et al., 1983]

Ungulinidae:

Diplodonta subquadrata [Vermeij et al., 1989]

Carditoidea. Carditidae:

Beguina diversicosta [Kojumdjieva, 1974]

Cardita spp. [Adegoke & Tevesz, 1974]

chamaeformis [Boekschoeten, 1967]

Cyclocardia subtenta [Colbath, 1985]

Venericardia greggiana [Kitchell, 1982]

V. serrulata [Taylor, 1 970]

Vetericardiella* [Kitchell, 1986]

Crassatelloidea. Astartidae:

Astarte spp. [Boekschoten, 1967; Kelley, 1989a]

Astarte triangularis [Smith, 1932]

Eriphyla striata [Taylor et al., 1983]

Lirodiscus tellinoides [Siler, 1965]

Nicaniella formosa [Taylor et al., 1983]

Crassatellidae:

Crassatella spp. [Taylor, 1970]

C. v/adosa [Sohl, 1969]

Crassatellites* [Kohn, unpub.]

Eucrassatella spp. [Kelley, 1982a]

Cardioidea. Cardiidae:

Acanthocardia tuberculata [Vignali & Galleni, 1986]

Cardium spp. [Smith, 1932]

politionanei [Kojumdjieva, 1974]

Cerastoderma edule [Bayliss, 1986]

Clinocardium nuttallii [Bernard, 1967]

Dinocardium robustum [Kornicker et al., 1963]

Fragum fragum [Vermeij, 1980]

Laevicardium aléñense [Vermeij et al., 1989]

Loxocardium bouel [Taylor, 1 970]

Parvicardium scabrum [Bayliss, 1986]

Protocardia hillana [Taylor et al., 1983]

Thetis laevigata [Taylor et al., 1983]

Mactroidea. Mactridae:

Mactra angulata [Taylor et al., 1983]

M. australis [Laws & Laws, 1972]

M. chiinensis [Vermeij et al., 1989]

M. fragilis [Paine, 1963]

M. stultorum [Vignali & Galleni, 1987]

Mactrellona exoleta [Vermeij et al., 1989]

Notospisula parva [Green, 1968]

Pseudocardium sachalinense [Vermeij et al., 1989]

Spisula elliptica [Bayliss, 1986]

S. solidissima [Franz, 1977]

S. subtruncata [Bayliss, 1986]

Tresus nuttallii [Reid & Friesen, 1980]

Mesodesmatidae:

Atactodea striata [Ansell & Morton, 1987]

Coecella chinensis [Ansell & Morton, 1987]

Donacilla angusta [Laws & Laws, 1972]

Ervilia ousilla [Hoffman & Szubzda, 1976]

E. dissita [Kojumdjieva, 1974]

[Begin Page: Page 192]

Solenoidea. Solenidae:
Ensis directus [Schneider, 1982]
Solen conradi [Colbath. 1985]
S. strictus [Frey et al., 1987].

Tellinoidea. Donacidae:

Donax spp. [Vermeij et al.. 1989]

D. faba [Ansell & Morton, 1987]

D. semistnata [Vignali & Galleni, 1987]

D. trunculus [Vignali & Galleni, 1987]

D. vittatus [Negus, 1975]

Plebidonax deltoides [Kitching & Pearson, 1981]

Psammobiidae:

Gari hamiltonensis [Hingston, 1985]

Tagelus peruvianas [Vermeij et al., 1989]

Scrobicularildae;

Scrobiculana plana [Richter, 1962]

Solecurtidae:

Solecurtus antiquatus [Kojumdjieva, 1974]

Tellinidae:

Arcopagia robusta [Vermeij, 1980]

Macoma albana [Colbath, 1985]

M. arctata [Colbath, 1985]

M. balthica [Commito, 1982]

M. calcárea [Aiken & Risk, 1988]

M. nasuta [Reid & Gustafson, 1989]

Palaeomoera inaequalis [Taylor et al., 1983]

Peronidia venulosa [Vermeij et al., 1989]

Quidnipagus palatam [Vermeij, 1980]

Scissulina' [Vermeij, 1980]

Tellina spp. [Vermeij et al., 1989]

T. donacina [Vignali & Galleni, 1987]

T. emacerata [Colbath, 1985]

T. lux [Broom, 1983]

T. planata [Kojumdjieva, 1974]

T. púdica [Broom, 1983]

7. pulchella [Vignali & Galleni, 1987]

T. tenuis [Ansell, 1982a-c]

Tellinella virgata [Nakamine & Habe, 1983]

Temnoconcha cognata [Vermeij et a!., 1989]

Circomphalus subplicatus [Hoffman & Szubzda,

1976]

Costacallista laevigata [Taylor, 1970]

Dosinia dunken [Vermeij et al., 1989]

D. lupinas [Vignali & Galleni, 1987]

Flaventia ovalis [Taylor et al., 1983]

Gafranum minimum [Smith, 1932]

G. pectinatum [Vermeij, 1980]

Gemma gemma [Wiltse, 1980a]

Gouldia minima [Vignali & Galleni, 1987]

Katelysia scalanna [Laws & Laws, 1972]

Kathennella angustifrons [Colbath, 1985]

Macrocallista nimbosa [Paine, 1963]

Megapitaria squalida [Vermeij et al., 1989]

Mercenaria mercenaria [Berg & Porter, 1 974]

M. campechiensis [Paine, 1963]

Meretnx lusoria [Vermeij et al., 1989]

Paraesa faba [Taylor et al., 1983]

Pelecyora trígona [Broom, 1983]

Periglypta reticulate [Vermeij, 1980]

Pitar spp. [Vermeij et al., 1989]

P. morrhuana [Jacobson, 1965]

Placamen subroboratum [Hingston, 1985]

Protothaca spp. [Vermeij et al., 1989]

P. staminés [Peterson, 1982]

Ruditapes philippinarum [Rodrigues, 1986]

Saxidomus giganteus [Bernard, 1967]

Sunetta gibberula [Hingston, 1985]

Tapes japónica [\-\amada. 1961]

T. philippinarum [Ansell & Morton, 1987]

Timoclea manca [Vermeij, 1980]

Tivela spp. [Vermeij et al., 1989]

Venerupis aurea [Vignali & Galleni, 1987]

V. senegalensis [Vignali & Galleni, 1987]

Venus multilamella [Kojumdjieva, 1974]

V. striatula [Ansell, 1960]

V. verrucosa [Vignali & Galleni, 1987]

Veremolpa miera [Mukai, 1973]

Glauconomidae;

Glauconome chinensis [Ansell & Morton, 1987]

Arcticoidea. Arcticidae:

Árctica islándica [Christensen, 1970]

Epicypnna angulata [Taylor et al., 1983]

E. subtruncata [Taylor et al., 1983]

Venilicardia lineolata [Taylor, et al., 1983]

Veneroidea. Veneridae:

Anomalocardia squamosa [Ansell & Morton, 1987]

A. squamosa [Taylor, 1980]

Aphrodina nitidula [Taylor, 1 970]

Bassina calophylla [Ansell & Morton, 1985]

Callistina plana [Taylor et al., 1983]

Calpitaria distincta [Taylor, 1 970]

Calva subrotunda [Taylor et al., 1983]

Chamelea gallina [Guerrero & Reyment, 1988a]

Chímela caperata [Taylor et al., 1983]

Chione spp. [Smith, 1932]

C. bastero^/ [Kojumdjieva, 1974]

californensis [Stump, 1975]

. cancellata [Paine, 1963]

C. subrugosa [Vermeij et al., 1989]

C. undatella [Peterson, 1982]

Order Myoïda. Myoïdea. Myidae:

Cryptomya californica [Watkins, 1974]

Mya arenana [Edwards, 1975]

Corbulidae:

Caestocorbula' [Kitchell, 1986]

Caryocorbula deusseni [Kitchell, 1982]

Corbula spp. [De Cauwer, 1985]

Corbula carinata [Kojumdjieva, 1974]

C. elegans [Taylor et al., 1983]

C. gibba [Vignali & Galleni, 1987]

C. idónea [Kelley, 1989a]

C. rugosa [Taylor, 1 970]

. trúncala [Taylor et al., 1983]

Notocorbula ephamilla [Hingston, 1985]

N. innerans [Maxwell, 1988]

Varicorbula amekiensis [Adegoke & Tevesz, 1974]

Vokesula aidrichi [Kitchell, 1982]

Hiatelloidea. Hiatellidae:

Hiatella árctica [Aitken & Risk, 1 988]

Panopea mandíbula [Taylor et al., 1983]

[Begin Page: Page 193]

Subclass Anomalodesmata. Pandoroidea. Periplomatidae:

Cochlodesma leanum [Rosewater, 1 980]

Pehploma spp. [Rosewater, 1980]

Poromyoidea. Cuspidahidae:

Cuspidaria cuspidata [Hoffman & Martinell, 1984]

Scaphopoda.

Dentaiiidae:

Dentalium complexum [Fankboner, 1 969]

D. bedensis [Kojumdjieva, 1974]

D. spp. [Yochelson et al., 1983]

Fustiaria miocaenica [Hoffman et a!., 1974]

Entalinidae:

Entaliopis brevis [Yochelson et al., 1983]

Gadilidae:

Cadulus* [Yochelson et al., 1983]